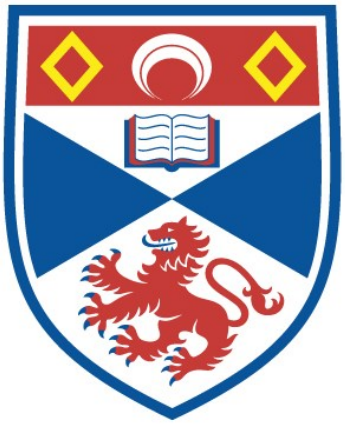
THE ECOLOGY OF A TIDAL POOL AT ST. ANDREWS, FIFE

David Edward Guthrie Irvine

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



1954

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Being a Thesis presented by David Edward Guthrie Irvine B.Sc.
to the University of St.Andrews
in application for the Degree of Ph.D.

ms 1944

Declaration

I hereby declare that the following Thesis is based on the record of work done by me, that the Thesis is my own composition, and that it has not previously been presented for a Higher Degree.

The research was carried out in the Gatty Marine Laboratory of the University of St.Andrews under the direction of Dr. M.C.H. Blackler.

Signed

Certificate

I certify that David Edward Guthrie Irvine B.Sc. has spent nine terms of Research Work under my direction and that he has fulfilled the conditions of Ordinance No.16 (St.Andrews) and that he is qualified to submit the accompanying Thesis in application for the Degree of Doctor of Philosophy.

Director of Research

Career

I matriculated in the University of St.Andrews in 1942. My course was interrupted by war service from 1944 to 1947, but led to graduation in 1950. This was followed the next year by the addition of Post-graduate Honours of the First Class.

I was admitted as a Research Student of the University of St.Andrews under Ordinances 16 and 61 as from 1st October 1951, and was awarded a University Post-Graduate Scholarship from the same date, during the tenure of which I undertook the research now being submitted for the Ph.D. Degree.

In March 1954, I was appointed a University Demonstrator of Agricultural Botany in the School of Agriculture, Cambridge, from 1st October 1954.

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I. INTRODUCTION

1. General

An intertidal rock pool provides a particularly interesting subject for ecological study, in view of the often widely different environmental conditions which may obtain within a relatively short space of time. While the pool is covered by the tide it becomes part of the sea bed, subject to the violence of wave action, the incursion of drift, debris, silt and wandering animals, and to a reduction in light intensity which may be considerable, depending on depth, turbidity and movement of the covering water. On the other hand, exposure of the pool by the ebbing tide leaves it an isolated, more or less sharply limited environment, in which conditions with regard to certain other factors, notably temperature, hydrogen ion content, dissolved oxygen and salinity, may vary widely. The nature and extent of these variations are mainly dependent on topography, period of exposure and prevalent atmospheric conditions, and the flora and fauna of a particular pool reflect to a large extent the conditions to which it is subject during this period of isolation from the sea.

2. Review of Literature

Investigations of rock pool ecology have on the whole been either general or limited to a very short period or to a very few aspects. Chapman (1941, p.356; 1946, p.636) gives a brief but excellent summary of the situation, and recent work has done little to alter it.

Large scale coastal surveys such as those undertaken in recent years by T.A. and Anne Stephenson and co-workers are naturally not concerned with such specialised habitats and have little or nothing to say about them. More intensive studies of relatively restricted areas of coastline (Rattray 1886c, Cotton 1912, Jónsson 1912, Muenscher 1915, Rees 1935, Gibb 1938, 1939, Srinivasan 1946, Rigg & Miller 1949, and many others) have usually included details of topography of pools within the area studied, together with lists of contained algae, usually correlated with tide level and sometimes with additional information concerning factors such as temperature variation and seasonal changes in distribution: Aleem (1950) has dealt similarly with marine littoral diatoms.

Papers dealing specifically with rock pools are relatively sparse, and the treatment has been too diverse to be readily summarised. Clapham (1926) gives a somewhat general description of the distribution and seasonal variation in the flora of pools and adjacent rock-surfaces near Bangor, County Down, but the inadequacy of the description of

environmental conditions involved somewhat limits the usefulness of the account for comparative purposes. Dunn (1940) gives a general comparison of the flora of pools at different levels on the shore of St.Andrews, Fife, with details of seasonal frequency and epiphytism of the species inhabiting them, correlated to some extent with mean temperature and sunshine conditions during the two spring seasons concerned.

Particular factors affecting the flora and fauna of rock pools have been studied more or less closely by several authors. Henkel (1906) paid particular attention to the structure of a series of rock pools at Port Renfrew, Vancouver Island, principally in relation to the faunas. Skinner (1905), in the same locality, had previously compared the floras of eight pools at different tide levels, taking into account location, exposure to wave action, shape and dimensions of the individual pools. Klugh (1924), at St.Andrews, New Brunswick, compared the flora and fauna of six similar pools at different levels, contrasting level, period of isolation, temperature, hydrogen ion concentration and salinity. Johnson and Skutch (1928), in their detailed study of the littoral vegetation of a section of the coast of Mt. Desert Island, Maine, paid special attention to tide pools, summarising the distribution of algae within the nineteen pools studied, measuring temperature and hydrogen ion content, and attempting to assess the environmental factors determining the observed variations in distribution.

Their work was, however, confined to the summer months, though covering several years of observation.

The first worker to make a detailed and comprehensive study of the variation of environmental factors in a tidal rock pool during exposure was Fischer-Piette (Fischer 1929), in the course of his important work on ecological factors governing the littoral region of the French side of the English Channel. He listed the flora and fauna of two intertidal pools at different levels and measured the reductive power, dissolved oxygen content, hydrogen ion concentration, salinity, water temperature and air temperature at intervals for as long as the pools were exposed during an entire day. Davy de Virville (1934, 1935), made an extensive study of the diurnal variations of temperature and hydrogen ion concentration in different types of rock pool both in summer and winter, dividing them into six distinct categories on the basis of his observations. More recently, Ambler and Chapman (1950) have made quantitative measurements of a number of factors affecting a series of tide pools near Auckland, New Zealand, over an entire year.

However, the majority of these workers tended to treat the pools studied as homogeneous units, an assumption which is approximately correct only for shallow, open pools. Lami (1931, 1934a and b, 1941), has been the first to make detailed studies of the variation of specific environmental factors within individual pools, and to discuss the effect

of such changes on algal distribution within the pool concerned. He investigated variations of hydrogen ion concentration, salinity and light in tide pools on the Breton coast, several of them with a topography remarkably similar to the general type of pool occurring in the area where the present work has been carried out. He also combined field observations with measurements using individual species under laboratory conditions, a technique carried yet further by Biebl (1937) in his close study of the flora of seven rock pools on the English south coast, in an attempt to discover the factors controlling distribution.

3. Aim of Work

The aim of the present work has been to study the distribution, reproduction and condition of the flora, and to a lesser extent of the fauna, of a particular pool over as long a period as possible, to note, and where possible measure, changes in environmental conditions obtaining in and around the pool over the same period, and to attempt to correlate the information obtained. For this purpose additional information has been collected concerning neighbouring pools, surrounding rocks, the St.Andrews marine flora and fauna in general, supplemented occasionally by reference to laboratory cultures.

It has not been possible to cover this field in its entirety with any degree of thoroughness: too minute and exhaustive an examination would for one thing defeat its own aims by interfering too gravely with the natural conditions obtaining in the pool. Attention has been concentrated on certain aspects, on the more prominent ecological and systematic groups, and on a limited number of the physical factors involved, in particular on topography, temperature and light. In order to present as complete an account as possible, however, all factors deemed likely to be of major importance are here discussed in general, in relation to previous work published on the subject, and to their possible effect on the pool and its inhabitants. An attempt is made, following the description of the plants and animals concerned, to outline their relationship to their environment and to each other, and to draw conclusions of more general application from this particular study.

II. ENVIRONMENTAL FACTORS

Many of the factors which have a vital influence on the flora and fauna of rock pools have already been mentioned in the introduction. Those discussed below are:- location and topography of the pool, period of exposure, desiccation, wave action, light, temperature, hydrogen ion concentration, dissolved oxygen concentration, salinity, other inorganic substances in solution, non-living organic matter in the pool, and biotic influences. It must be emphasised that the effects of these factors cannot be considered entirely separately, since their variations are often closely inter-related, and that not all of the above have been measured quantitatively during the course of the present work. All times mentioned are given as Greenwich Mean Time on the twenty-four hour clock.

1. Location and Topography of the Pool

The particular pool examined is situated on the Hind Rock (Fig.1), a long sandstone ridge which runs approximately East/West at a slightly oblique angle to the shore. This ridge is composed of very friable sandstone, the strata of which are tilted at an angle of about 30°, giving it a steep, much-eroded northern face and a more or less uniformly sloping southern side. It is weathered to form several series of pools which in general conform to the direction

and slope of the ridge, i.e. the long axis lies East/West and the bottom of the pool slopes gradually from the north to a steep or overhanging southern bank. This conformation is modified in places by outcrops of more durable, iron-impregnated rock.

The pool in question (Figs. 3 - 7) conforms to the general type. It lies on the crest of the ridge, 430 ft. (130 m.) from its landward end, and measures 3.7 m. by 1.5 m., with a maximum depth of 24 cm., a surface area of 3 sq.metres and a volume of some 350 litres. The principal topographical features are shown in the chart (Fig.8a) and various transects (Fig.8b - e). The south bank does not rise far above the water level and the overhang is slight to within a few centimetres of the bottom, where it is in places sharply undercut to a distance of up to 30 cm. (Fig.8c). The bottom slopes from the shallow northern side to the deeper southern one, the more or less uniform gradient of about 30° being interrupted by a series of ridges, the longest running almost the full length of the pool though only about 8 cm. high. A much higher shelf of rock occupies the southernmost part of the pool.

The above measurements refer to the dimensions of the pool when first left by the tide. During the period of exposure the level falls continuously, at first rapidly as water escapes along the outlet at the landward end of the pool, then slowly and fairly steadily at an average rate of

about 2 mm. per hour, increasing as the surface area is reduced. This is due mainly to direct escape of water through the porous sandstone, aided no doubt by minute cracks and fissures, and over the surface by capillarity amongst matted algal fronds, and partly to evaporation from the surface and exposed algae. Since the extent of this fall of water level depends largely on the period of exposure its considerable ecological significance will be dealt with in the following section.

The very friable nature of the sandstone has several important consequences. As Allen (1899) has pointed out, the texture of the substratum is more important than its geological character. However, since these effects are very closely linked with wave action they will be considered under that heading.

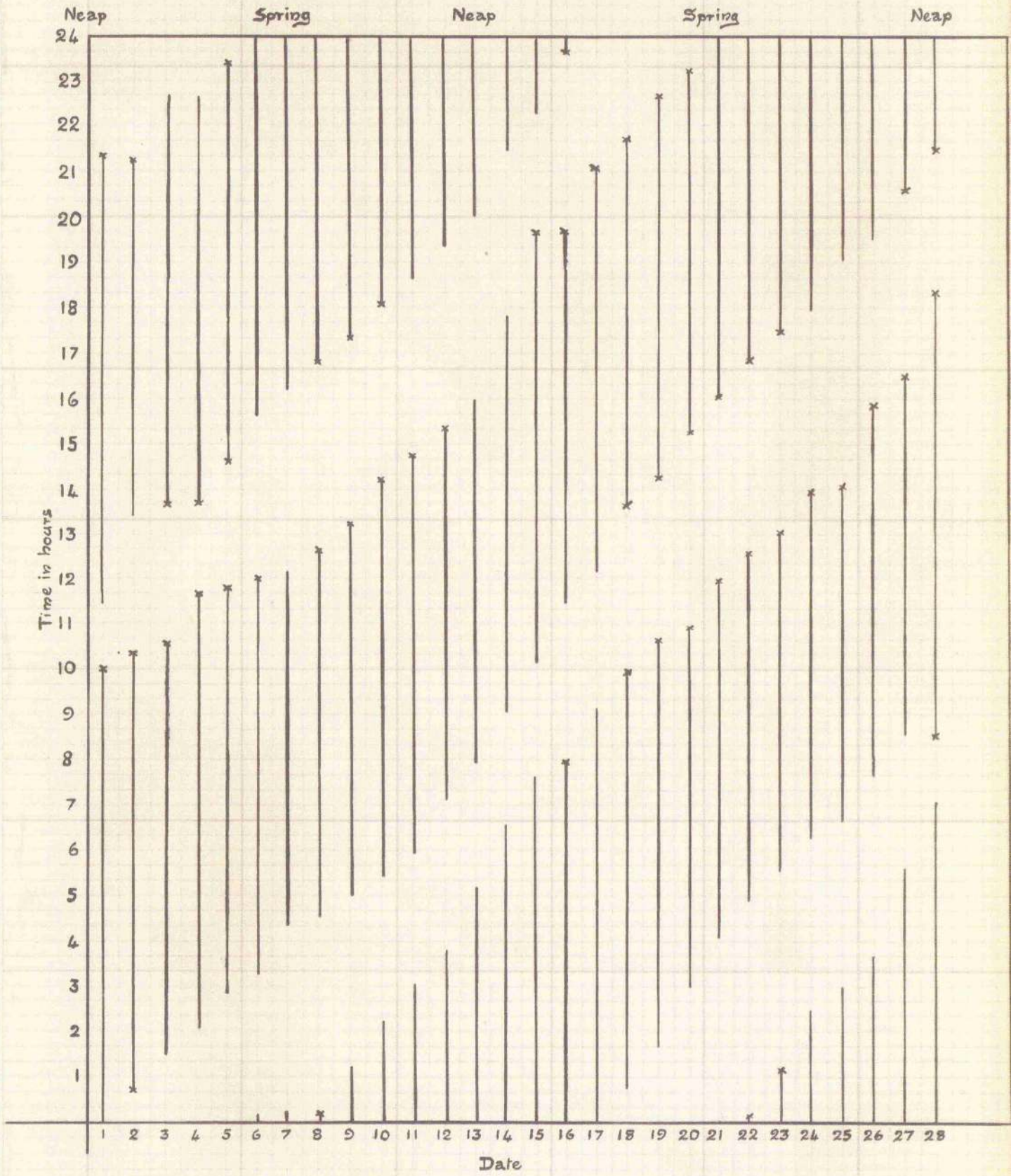
2. Period of Exposure

The following data on tide levels for St.Andrews have been obtained from the Fifeness coastguard station, and refer to height above chart datum.

Mean High Water of Spring tides (M.H.W.S.)	15.7 ft. (4.53 m.
Mean High Water of Neap tides (M.H.W.N.)	12.7 ft. (3.88 m.
Mean tide Level (M.L.)	8.7 ft. (2.65 m.

The height above chart datum of the pool itself

(measured with reference to a bench mark 13.2 ft. above ordnance datum (Liverpool) (20.4 ft. above chart datum) at the harbour), is 11.9 ft. (3.62 m.). This is sufficiently close to M.H.W.N. level to ensure that during neap tides the pool is exposed for a very long time, and, given a combination of calm weather and extremely poor neap tides, the sea may not enter it for several consecutive days. This is obviously a factor of very great importance; as will be shown later the whole nature of the flora, and to a lesser extent of the fauna, may be rapidly changed by conditions during these few critical days, and the effects may be traced for many months. During more normal conditions however, the pool is left by the tide for some eight hours at a time, though in rough weather or with a heavy swell the effective period of coverage may be increased by an hour or more. The accompanying chart (text-fig.1) shows periods of exposure during a lunar month without exceptionally poor neap tides. The crosses represent direct observations of times of the tide entering or leaving the pool: in other cases the time has been calculated from a knowledge of predicted tides and weather conditions, usually aided by direct observation as near the estimated time as possible (with practice considerable accuracy had been attained in such predictions). The irregularities, particularly apparent early in the month, were caused by strong winds and rough seas, but in general the weather was calm, and the figure



Text-fig.1. Chart showing the time of exposure of the pool during November 1953. The average daily exposure was 16 hrs. 55 min.

demonstrates quite well the short period of coverage during neap tides relative to that of spring tides.

3. Desiccation

As Isaac (1938) has pointed out this is the most important factor of all for algae growing above the infra: :littoral fringe. It is obviously a subsidiary factor where the flora of pools is concerned, however. In this particular case the continual drop of water level during normal exposure subjects the fringing plants to a certain risk of desiccation, countered, however, by water held and drawn up amongst the silt, algal filaments and superficial rock particles by capillarity, and this factor only becomes lethal under neap tide conditions. Plants which are exposed to this risk in the normal course of events are protected in various ways (e.g. by extra thick cell walls, copious mucilage production, low compact growth form): it is the species and individuals normally submerged which suffer most when unexpectedly exposed for any length of time.

4. Wave Action

The effects of wave action are primarily mechanical, though the effective increase in tide level may also be important, particularly at the time of neap tides. The

mechanical effects depend both on the actual intensity and on the frequency of wave shock (Evans 1947). The pool is sheltered from the full impact of waves, which generally break against the steep northern face of the ridge and, in rough weather, first enter the pool on the northern side and sweep across it (Figs.9 and 10). In calmer weather entry is from the seaward and drainage from the landward end, so that silt gets little chance to settle in these parts. As the tide rises higher the waves curling round the Hind Rock and those breaking directly across meet along a line passing over the pool, which is therefore subjected to considerable turbulence under such conditions.

The most noticeable effect is the rapid rate of erosion. Some evidence of this can be obtained by comparing the topography of the pool in Figs.14 and 15 after a lapse of only two years. During the period for which the pool has been studied sections of rock have been torn away from the northern and landward sides of the pool, greater or smaller areas have been suddenly denuded to the bare rock, and the central ledge has been relentlessly eaten away. Thus new areas for colonisation are being perpetually prepared and weak, moribund or isolated plants removed, while loose rock and larger pieces of debris are rarely left for long even in the most sheltered parts of the pool. The silt stirred up by the waves or formed from the eroded rocks abraids the substance of the more delicate plants

and probably explains the absence of many animals with particularly vulnerable tissues. It must also cut down available light to a considerable extent, a point more appropriately dealt with in the following section.

5. Light

The importance of light as a factor determining the distribution of algae has long been recognised, and perhaps in some cases over-emphasised, since it is difficult to segregate effects due primarily to light conditions from those resulting from associated conditions of, for instance, temperature and desiccation. It is nevertheless of considerable influence in affecting the distribution, growth and periodicity of algae. Submarine illumination has been measured in various ways by many workers, but only for the deeper waters of the open sea or the infralittoral, and not hitherto for littoral rock pools. Levring (1947) has summarised earlier work on this factor and studied photosynthesis of various algae in the sea itself, producing evidence to support the view that both intensity and spectral composition of submarine radiation influence marine algal distribution. He indicated the importance of the various sensitizers (notably phycoerythrin and fucoxanthin) in adapting algae to function best at different light intensities and with light of different spectral compositions, and showed the close

relationship between temperature and illumination in determining the balance between photosynthesis and respiration, on which the rate of growth must ultimately depend.

The shallow, open nature of the pool did not lend itself to accurate measurement of light under the various conditions to which it is subjected. Some attempt has been made, however, to obtain approximate measurements for comparative purposes in various parts of the pool during periods of exposure, using two selenium photronic cells, one fitted in a watertight case of lacquered brass, with perspex top for underwater measurement, the other exposed on a neighbouring rock to record surface illumination, connected to a micro-ammeter and with a resistance which could be included in the circuit for use in bright sunshine. A diagram of the circuit is shown in Fig.11. Both were carefully levelled to a horizontal position before use. The instruments were calibrated as accurately as possible by comparison with a Weston photo-electric light meter. The actual figures thus obtained, though necessarily somewhat unreliable because of the crude nature of the apparatus, nevertheless give a better indication of comparative conditions than could a purely subjective estimation.

Variations in strength and duration of light to which different parts of the pool are subjected may be brought about in many ways. The most important are seasonal. The short winter day and low zenith of the winter sun not only

cut down the amount of light available in all parts of the pool but increase the area within it which is shaded by the southern banks from direct sunlight. In midwinter the sun at its zenith is only 10° above the horizon and sets for the pool behind the cliffs at about 12.30 hrs., giving the pool a possible maximum of about 3 hrs. of direct sunlight of a maximum intensity of about 1,000 foot candles, and about 7 hrs. of daylight, while even at midday about three-quarters of the pool is shaded by the southern banks and receiving something like 80% or less of the available light. The extent of shading is shown by Fig.12; under these conditions the vegetation is predominantly of red algae. In midsummer the sun at its zenith is 57° above the horizon and the pool may theoretically receive a maximum of about 12 hrs. of direct sunshine and about 18 hrs. of daylight, while the shaded area within the pool is very much reduced.

More erratic factors are winds and storms. During exposure the ripples caused by the wind on the surface have been found to cut down the light by about 1% for slight breezes. The effect is undoubtedly greater for stronger winds, but it is then difficult to isolate the effect due to this factor. While the pool is covered violent movements of the water stir up quantities of silt which must cut out a very high proportion of the incident light, but unfortunately conditions at such times do not permit of measurements being made. The heavier particles settle relatively quickly in

the exposed pool, but the water may remain visibly cloudy for many hours. Such measurements as could be made have shown that within about 1 hr. of exposure a point 7.5 cm. deep in the open pool received 91% of the incident light, while another 14 cm. deep received only 87%; about half an hour later a point 2 cm. deep was getting 96% while another at a depth of 16 cm. still received 91.5% of the light incident on the surface.

The relationship between light intensity and distribution and growth of the algae cannot usefully be considered without reference to temperature variation and the particular species concerned, and is accordingly dealt with in a later section.

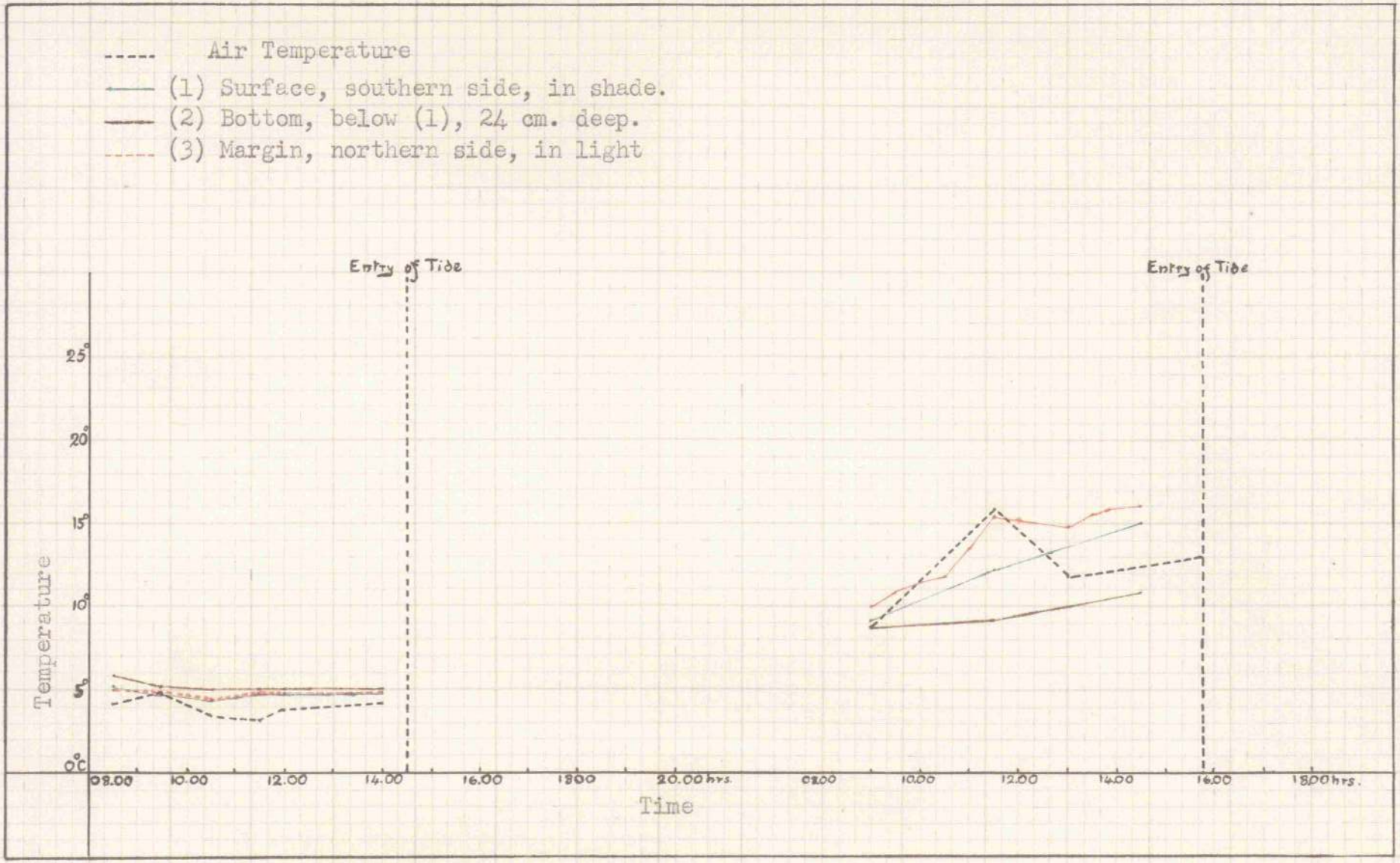
6. Temperature

This is obviously one of the most crucial environmental factors for both plants and animals. Levring (1947) has emphasised its importance in determining the assimilatory surplus which plants must form to meet growth requirements: increased sunlight leads to a greater rate of photosynthesis, but beyond a certain point this increase is more than balanced by the greater rate of respiration brought about by the accompanying rise in temperature. The changes in rate and nature of metabolism may prove lethal both under extreme temperatures and in conditions of a very rapid rate of change,

and the latter is considered by Allen (1899) as of greater importance. The limits which various species can withstand differ (Allen 1899, Biebl 1937), while specimens of the same species of alga or animal from different bathymetric levels also show variations in lethal limits of temperature (Shelford 1915). Temperature has also been shown to be a major factor in determining sexual activity of animals (Orton 1920): its influence in this respect on algae is not so clear-cut and is probably secondary to that of light. Temperature differences also lead to differences in density and hence to the formation of more or less stable layers of water. This is of course more important where much greater depths of water are being considered, but cannot be entirely neglected in the present case, particularly when reinforced by variations in salinity.

Variations in temperature from one part of the pool to another and at different seasons form a very complex pattern. They depend in the first place on the temperature of the surface seawater immediately before the pool is left by the tide. Careful measurement has shown that even on a calm day mixing is sufficiently thorough to ensure virtually isothermal conditions on initial exposure. Thenceforward, however, until the return of the tide, conditions may vary considerably in different parts, depending on intensity of sunshine, degree of shading, depth, amount of water movement, influx of rain water and rate of evaporation. With all these

variable and secondary factors it is somewhat difficult to produce a clear picture of what actually occurs. Extensive and detailed records, involving many hundreds of measurements in and near the pool, have been kept: the principal points selected for measurement were:- in air just above the southern bank, in the surface water of the sea (at a depth of about 10 cm.) and at three points within the pool itself - (1) just below the surface on the southern side in the shade of the highest part of the bank (2) on the bottom immediately below that point (at a depth of about 24 cm.), and (3) immediately below the surface on the shallow northern side. Sea temperatures taken by the lighthouse staff at the Bell Rock (14½ miles from St.Andrews) and air temperatures recorded daily for St.Andrews were also available for comparison. These show that the highest air temperatures, both mean and maximum, occur in July, and the lowest, more erratically, about January, while surface sea temperatures, reach their maxima and minima in August and February respectively. The waters around the Hind Rock show a similar trend, but naturally with somewhat wider fluctuations. Within the pool fluctuations may be considerable, especially for the surface waters, as is shown by text-fig.2. Except under neap tide conditions the diurnal variation in the deepest part is rarely greater than about 4°C, while on the shallow illuminated side it may amount to as much as 12°C. on a hot summer's day. The algae left above the water level



Text-fig.2 Temperature variations within and near the pool on a day in winter (23rd January 1954), and in spring (29th April 1952), showing the wide differences in temperature from one part of the pool to another developing in the latter period.

may be exposed to a still greater range of temperature. The pool has never been observed to become fully frozen over, though the lowest temperatures recorded (-1.5°C. at the surface and -0.5°C. in the deepest part at 0900 hrs., 2nd March 1954) are little above the freezing point for salt water (about -2.0°C.). The coldest periods are normally immediately before sunrise. The highest temperatures are attained in July and August on calm sunny days, when a maximum temperature of as much as 25°C. may be reached in the course of an afternoon. Temperature variation within the pool is little during cold weather, rarely more than about 2.0°C., but during the summer and early autumn the lighter warm water does not mix to any extent with the colder water underneath, and there may be a difference of as much as 10°C. or more from one part to another. Thus at 1430 hrs., 15th May, 1952, the temperature of the water underneath the overhanging southern bank was only 14.5°C. and at the same time was 25°C. on the shallow northern side. Particular effects of temperature range on the flora and fauna of the pool will be dealt with later: broadly speaking, very low temperatures slow down animal activity but appear to be rarely lethal for any of the inhabitants of the pool, whereas high temperatures are probably largely responsible for the relative barrenness of the pool during mid-summer.

7. Hydrogen ion Concentration

Many workers have measured the hydrogen ion concentration of the water left in rock pools during the period of exposure. It has been shown that the changes may be very rapid, e.g. from 8.1 to 10.0 in 4½ hrs. (Davy de Virville 1935), and that the rate and extent of rise depends on the relative rates of photosynthesis of the algae and respiration of both algae and fauna. Thus Klugh (1924) showed that the measured value for a series of pools was to some extent dependent on the relative proportions of plant and animal life. Atkins (1922), Davy de Virville (1935), Lami (1934a) and others have shown that the maxima attained differ for various algae under the same conditions. The extensive measurements made by Davy de Virville (1935) indicated that the rate of rise and ultimate maximum attained depended on the quantity of algae, their physiological condition, the dominant types and the amount of insolation, but was practically independent of temperature.

Since the hydrogen ion environment is actually regulated by the algae themselves its influence is difficult to interpret. Atkins, Lami and Davy de Virville (loc.cit.) have all suggested that it might be of importance in influencing distribution, e.g. in hindering or favouring development of spores of particular algae, especially of epiphytes, but it is difficult to prove this point.

Measurements have been made occasionally in different

parts of the pool and under varying conditions. Samples of sea water were drawn off by a glass syringe which was emptied beneath a layer of petroleum ether into large specimen tubes. These were tightly stoppered, and the hydrogen ion content measured as soon as possible, using a Cambridge pH meter. Results have shown that on dull winter days the hydrogen ion content, even in the afternoon after several hours of exposure to the diffuse daylight, was more or less uniform throughout the pool and little above that of the sea (e.g. 8.4 at 1450 hrs. on 12th December, 1953), but on a sunny spring day could rise quite rapidly in the shallow parts (e.g. 7.93 at 0930 hrs., 8.86 by 1200 hrs. on 3rd March, 1951) and differ considerably between deep shaded and shallow sunny parts of the pool, e.g. 8.52 on the bottom below the southern bank, 8.61 on the surface above that point, and 8.93 on the shallow northern side, at 1530 hrs. on 24th February, 1953. At night the concentration may fall sharply, as found by Fischer-Piette (Fischer 1929): thus at 2200 hrs. on 24th February 1953, it measured only 7.58 in the deepest part of the pool. Very high values as reported by Davy de Virville (loc.cit.) have not been encountered, but the same trends, of very rapid rise to a high maximum amongst Chlorophyceae and of a slower rise to a lower maximum amongst Rhodophyceae, have been observed. The low values of early winter may be attributed to the generally poor condition of the algae, the preponderance of Rhodophyceae and a relatively greater pro: :portion of animals to plants.

8. Dissolved Oxygen Concentration

This factor was not studied quantitatively. It is controlled by the rate of photosynthesis, the proportion of animal to vegetable life, depth, amount of water movement and temperature. As Fischer-Piette (Fischer 1929) and Lami (1934c) and Ambler & Chapman (1950) have shown it varies in the same manner as does the hydrogen ion content, indicating that the primary controlling factor is likewise the relation of photosynthesis to respiration. The results obtained by Rattray (1866b) in his experiments on the evolution of oxygen by individual algal species may also be taken to support this hypothesis. Lami (1934c) suggests that the oxygen content attains a maximum specific to the alga concerned.

In the pool the release of oxygen is often vigorous. The resulting gas bubbles are dangerous to many of the smaller animals, which are carried helplessly to the surface and are often unable to submerge again. This happens particularly often to chironomid larvae and to various species of amphipods.

9. Salinity

Variations in salinity may be expected to occur either as increases through evaporation during periods of prolonged exposure to intense sunshine or as decreases through heavy rainfall. Measurements have been taken under various conditions, using the international standard salinity apparatus.

These indicate that, even during prolonged exposure, evaporation does not produce any significant concentration. During neap tides in April exposure to bright sunshine for seven hours had only increased the chloride concentration from 18.95 to 19.09‰. This also shows that the drop in water level during exposure must be primarily due to direct water loss through the fissured and porous rock rather than by evaporation. Klugh (1924) found similarly negligible increase in concentration for a pool exposed to seven and a half hours of intense sunshine.

Decrease in salinity is likely to be a much more variable and important factor. There is little direct drainage of rain water into the pool from surrounding rocks, but the relatively large surface area leads during periods of heavy rain to the formation of a superficial layer of water of very reduced salinity. This is accentuated by the constant seeping away of the water of the lower layer, and is particularly striking when heavy rains accompany extreme neap tide exposures. Such conditions occurred on the 29th of March, 1954; when between 0800 hrs. and 2030 hrs. the chlorinity of the water about 1 cm. below the surface fell from 18.10‰ to 7.62‰, yet remained at 18.21‰ for the deepest part of the pool, a remarkable variation much greater than those recorded by Lami (1931). This implies that the algae fringing the pool must be euryhaline species capable of enduring submersion in water of considerably lowered salinity

for at least several hours at a time, and such is found to be the case, as will be shown later.

10. Other Inorganic Substances in Solution

Many measurements have been made of the amount of various essential or toxic substances present in solution in sea water, but the results obtained apply largely to the open sea or to rather specialised localities. Harvey (1926) observes that the inorganic salts necessary for plant life are always present in sea water in ample amount, except for phosphates and nitrates and possibly iron. The proximity of town sewage effluents and the abundance of sea-bird excreta on the Hind Rock render it unlikely that any of these essential constituents are ever in short supply for long enough to be effective limiting factors. A toxic concentration of certain substances is perhaps more possible, but no mortality likely to be caused by such agency has so far been observed. Sewage effluents seem occasionally lethal to algae at lower level pools and channels near the Hind Rock, but have no noticeable effect on the algae of the higher levels. Soot from the nearby city gasworks is often deposited in some quantity on the surface of the water. Okamura et al.(1926) have found that soot particles deposited on Porphyra tenera Kjellm. in Tokya Bay absorbed sufficient sulphur dioxide from the polluted atmosphere to kill the neighbouring cells: no effect of this

nature has been observed on the Ulva, Enteromorpha and other algae fringing the pool.

11. Organic Matter

Organic matter not directly associated with living organisms may be present as detritus and drift material of various kinds, as particulate suspensions and in solution. Possible sources are (1) external, as debris and sewage brought in by the tide and, during long exposures, sea-bird excreta and drowned insects, (2) internal, through death and decay of plants and animals, secretion, excretion, and cell damage by attrition or animal attack. Possible effects are provision of food for various organisms and, secondarily, lowering of hydrogen ion content and poisoning of the water through putrefaction.

Within the pool the amount of organic detritus present is somewhat variable. There is generally very little during winter and early spring, except for short periods following storms during neap tides. The increasing coverage of algae, and particularly the growth of large entwining masses of Rhizoclonium implexum, leads to considerably more debris being trapped and held in the pool during the late spring and summer, while the high mortality during extreme neap tide conditions also increases the quantity of decaying organic material present at such times. The larger littorinids appear to

feed mainly on algal debris washed into the pool, and it is probably an important source of food for many amphipods and annelids, while there are numerous suspension feeders (lamellibranchs, sponges, and others) in the pool fauna.

The organic matter dissolved in sea water has been measured in various ways by different workers. Fischer-Piette (Fischer 1929) measured the reductive power as a qualitative measure of the amount of dissolved organic matter present. He found that it varied irregularly during exposure of a pool, rising during the day but not at night, possibly, as he suggests, through excess photosynthesis taking place. Apart from toxic effects this is probably unimportant as a direct environmental factor, for Keys et al. (1935) have postulated that dissolved organic material if not perhaps wholly out of organic circulation is at least not ordinarily a major link in the food cycle in the sea. Pollution and putrefaction have not so far appeared to occur to any lethal extent; under the conditions which would favour such processes - prolonged neap tide exposure and high temperatures - the danger of complete desiccation is probably much greater.

12. Biotic Effects

(a) Interference by terrestrial fauna

For the pool this means essentially interference by sea-birds or by human activities. Various insects can be found drowned in the pool during the summer, but they can hardly be considered numerous enough to have any important effect. On the other hand sea-birds, mainly gulls and eider ducks, frequent the Hind Rock in large numbers, usually resting on the surrounding rock but occasionally wading or swimming in the pool. The possible importance of their abundant excreta has already been mentioned: to this may be added the occasional effects of stirring the pool water and disturbing the fauna, but these are relatively slight. A more important activity might be the destruction of larger animals by small shore birds when the pool is partially dried out during neap tides: though this seems likely there is no direct evidence that such destruction occurs, and in any case for many of these animals (annelids, nemertines, crustaceans) other conditions at such times might well prove fatal.

Human interference may be divided into the general and the individual. In the former category sewage and smoke pollution have already been mentioned. Smoke may also cut down light and even raise the temperature of the air in the vicinity of the pool to a marked extent, but these are too infrequent occurrences to require consideration. The nature and position of the pool makes it unlikely to be subject to

casual interference by individuals, and there seems no reason to suspect that this has at any time occurred during the period of observation. A much more serious problem has been the interference inevitable to prolonged and close observation of the pool. This has been reduced as far as possible by relying where practicable on observation *in situ* rather than on collection of material for laboratory examination, by avoiding shadowing or disturbing the pool more than was absolutely necessary, and wherever possible by removing parts only of plants for identification or check of reproductive condition, and returning to the pool animals removed for identification or measurement. This in turn limited the type of observations which could be made. For instance many burrowing animals and species represented only for short periods may well have been missed through reluctance to damage or disturb the pool overmuch by a thorough search. Thorough examination of particular communities was made difficult because so little material could safely be removed from one plot at a time, and regeneration and recolonisation were as far as possible studied following the effects of natural damage. It is believed that such destruction as was inevitably done would in most cases be similar to that produced by more normal hazards and proportionately slight, except in the rare event of clearance for examination of a quadrat, and these particular cases are discussed in detail in a later part.

(b) Inter-relationships of plants and animals

The various possible inter-relationships have been well summarised by Allen (1899). He points out that an advantageous influence is exercised by one organism or another when it (a) serves as a food supply, (b) provides a fixed base for attachment, (c) provides a movable base, thus extending the feeding grounds of the fixed organism, (d) brings food to the other organism, (e) provides shelter or concealment from enemies; a disadvantageous influence is exerted when it (a) preys on the other organism, (b) fixes on the latter in a way which brings about its destruction, (c) competes for a limited food supply or amount of fixing space. These few categories cover an infinite variety of subtly intergrading relationships, many of which are touched on in the following descriptions of the flora and fauna. Others are discussed more fully in the section dealing with particular communities, and the spatial relationship of algae and their epiphytes is considered important enough to merit a section to itself. Here it is perhaps sufficient to point out that the pool algae in general have three distinct stages at which the influence of other organisms may be critical. (1) As motile or drifting spores or gametes they are very vulnerable to attack, particularly by ciliates (which are always numerous amongst the motile Enteromorpha spores), while they are also liable to be engulfed by the numerous sedentary suspension feeders. (2) As settled spores and

sporelings they may be denied suitable environmental conditions by overcrowding, shading and possibly unfavourable hydrogen ion concentration established by neighbouring plants and sedentary animals, or may be destroyed by detritus feeders or browsing animals, particularly gastropods.
(3) Finally, as adults they may be weakened and overburdened with epiphytes to a point at which they are readily torn from the substratum by water movement.

III. FLORA OF THE POOL

The flora is both diverse and abundant, exhibiting striking variations in nature and state of growth at different seasons of the year. The course of these changes has been followed by means of notes, photographs, herbarium specimens, monthly vegetation charts (Fig.13) and a number of transects (Figs.16 and 17).

As this microcosm shows many parallels in its ecological structure with that of the shore in general, terms applied to these larger ecological units as defined by Feldmann(1951) are here applied in much the same sense, distinguished in this special context by the prefix micro-. Thus the position of the water level of the pool demarcates micro-zones somewhat analogous to the zones or belts due to tidal range on the shore. It is misleading however, to strain the analogy too far: the association is described by Feldmann as a subordinate unit of the facies, but here the micro-facies, which, like the corresponding larger units, is distinguished by the nature of the substratum, is subordinated to the micro-association, which is determined primarily by exposure to light. Finally the general term community is here used for the most homogeneous units, assemblages of plants and animals dominated by one or more algal species, occupying a specified type of habitat. The distribution of the principal communities is shown in Figs.14 and 15.

1. Life-forms

In defining and describing these particular ecological units it is essential to consider the life-forms of the characteristic algal species involved. The terms employed here for the most part follow the usage of Knight and Parke (1931) and Feldmann (1937), but with a rather more restricted application to suit this very specialised and limited environment.

A. Plants present throughout year

1. Individual plants persistent

(a) Growth and regeneration persistent throughout year ..... Perennials

(b) Growth and regeneration inhibited at certain seasons or under certain conditions ... Pseudo-perennials

2. Population maintained by successive crops of relatively short-lived individuals ..... Ephemerals

B. Plants present in macroscopic form for part only of year, individuals completely removed at end of growth period ..... Annuals

C. Plants of rare, irregular and generally short-term occurrence ..... Casuals

It must be pointed out, however, that the same species may fall into two or more categories in different parts of the pool and under varying conditions. Thus Fucus species are perennial round the border of the pool but largely annual where growing permanently submerged, and Polysiphonia nigrescens

is generally pseudo-perennial, but occasionally becomes annual through extermination by very adverse conditions.

2. Bionomic Divisions

Three micro-zones may be recognised in the pool vegetation, namely the exposed, fringe, and submerged micro-zones. These are usually very clearly delimited, and are related to the water-level within the pool.

I. The exposed micro-zone is emergent from the moment that the tide leaves the pool. It is dominated by a perennial growth of Fucus plants, relatively short and sparsely branched specimens of F. spiralis and F. vesiculosus var. evesiculosus on the northern side (Fig.19), and rather more luxuriant growth, with occasional F. vesiculosus var. vesiculosus, on the southern side (Fig.18). On both sides there is an undergrowth of very short, much-branched algae, principally Ceramium shuttleworthianum and Cladophora rupestris, intermixed with Rhodochorton floridulum.

II. The fringe micro-zone is markedly different on the two sides of the pool. It covers the area which is submerged when first the pool is left by the tide, but which is more or less rapidly exposed as the water-level within the pool falls until replenished by the incoming tide. During heavy rains this micro-zone may be immersed in a layer of water of very low salinity, and it is probably significant that the dominant algae are pronouncedly euryhaline. The

virtual absence of Rhodochorton floridulum is particularly striking. On the exposed side there is a perennial or semi-perennial covering of minute growths of Cladophora rupestris interspersed with patches of bare rock and the ephemerals Ulva lactuca var. rigida and Enteromorpha spp. During early spring U. lactuca var. latissima becomes not infrequent, and in late spring and early summer the entire micro-zone on the northern side is dominated by a strong growth of Enteromorpha spp. (Fig.19). A few small fucoids also occur here. On the shady southern side there is a perennial (or in parts semi-perennial) covering of large, healthy Cladophora rupestris both above and immediately below the water-line (Fig.18).

III. The submerged micro-zone is an area within which conditions vary considerably from part to part, and it is accordingly considerably subdivided, primarily into the open-pool and shade micro-associations, the latter being shadowed by the steep southern banks or the ledges within the pool. Both show striking seasonal variations in form and type of vegetation, but broadly speaking the former is characterised by Rhodochorton floridulum and various species of Ulvaceae, the latter by a very diverse vegetation in which Rhodophyta tend to dominate.

(a) The Open-pool micro-association is again divided into silted and silt-free micro-facies.

(i) The silted micro-facies is dominated by Rhodochorton floridulum, which carpets the bottom in a loose felt of silt and interlaced filaments with frequent short, erect tufts, particularly prominent in late winter and early spring (Fig.21). There is also a small community of stunted, densely-branched Cladophora rupestris plants, perennial or pseudo-perennial, which has maintained itself with little difference in size throughout the period of observation. Presumably it became established during a period of exceptionally favourable conditions and its presence may be regarded as wholly fortuitous, since its habitat seems in no way different from the surrounding area. The aspect of this micro-facies is very variable, due to the presence of ephemeral Enteromorpha species (Figs. 28-32). During winter and early spring these are represented by small narrow-fronded plants of E. compressa scattered rather sparingly amongst the Rhodochorton. As the spring advances this vegetation becomes markedly denser (Figs.20, 22, 24, 25), the individual plants being bigger and more rapid of growth and large plants of E. linza and E. intestinalis becoming increasingly prominent. The vegetation may show sharp set-backs during neap-tide exposures, due to wholesale sporing or actual destruction of the plants, but reaches a peak during May and June. The summer form of E. linza then disappears and typical E. intestinalis

plants become less numerous, while E. compressa plants luxuriate only as epiphytes on Cladophora and Fucus.

(ii) The silt-free micro-facies occurs more or less permanently at the ends of the pool, where the inflow and outflow of water effectively prevent the accumulation of silt, and transiently where the protecting layer of silt and algae is removed by storms or other agencies. The more permanently bare areas are dominated by Ulva lactuca var. rigida, together with a variable amount of Enteromorpha compressa, and all provide a suitable substratum for many of the more prominent annuals, such as Acrosiphonia centralis, Monostroma grevillei and Scytosiphon lomentaria.

(b) The shade micro-association can be divided into silted, silt-free and ledge micro-facies. There is no sharp line of demarcation between open-pool and shade micro-associations, and indeed as spring advances and shade decreases in the pool the former tends increasingly to encroach on the latter.

(i) The silted micro-facies, as in the open-pool, is carpeted by a mat of entwined filaments of Rhodochorton floridulum, but with increasing shade this becomes largely supplanted by a stunted growth of sterile Sphacelaria pennata var. fusca and patches of non-thalloid Codium (the taxonomic status of this Codium is discussed later), all generally heavily overgrown with

diatoms, dominated in parts by well-defined communities of Cladophora rupestris and Polysiphonia nigrescens (Figs.22 and 23). The former is very much better developed than in the open-pool community, but both are heavily covered by epiphytes and sedentary animals. These communities are considered in more detail in a later section.

(ii) The silt-free micro-facies is marked by the increasing number of the small perennial rosettes of Laurencia hybrida. The rock is encrusted with corallines, Lithothamnion lenormandii and Corallina officinalis. The latter is usually so covered with closely matted epiphytes that it might be better considered as part of the silted micro-facies. These merge into the ledge micro-facies or peter out into a fringe of diatoms and poorly developed casuals under the overhanging parts of the banks. The triangular shelf on the southern side of the pool requires special mention. It is washed free of silt and during the winter, is well shaded, but its shallowness and exposure to light and neap tide desiccation in spring and summer allow of a particularly anomalous, varied and rapidly changing vegetation. Annuals such as Dumontia incrassata, Monostroma grevillei and Acrosiphonia centralis are often especially well developed here.

(iii) The ledge micro-facies comprises the vertical or steeply sloping faces of ledges and banks, all facing approximately north and therefore shaded (Figs.22-25). The closely matted growth holds a considerable quantity of silt, but much less than in the bottom vegetation. The principal communities are dominated by Corallina officinalis and Codium respectively. The Corallina (Fig.25) is shorter, less luxuriant and generally not so heavily covered with epiphytic Sphacelaria pennata var. fusca as when growing on the bottom of the pool. The Codium (Fig.33) is pseudo-perennial, forming thick, mossy growths of vertical filaments arising from inter: ;laced horizontal ones from about July to March, rarely with a very few short, compact thalli in winter and early spring. A third important species is Polysiphonia urceolata, a pseudo-perennial forming conspicuous clumps of short, erect, sparingly branched fronds in winter and spring. The creeping filaments of both Codium and P. urceolata are generally abundantly intermixed with the basal parts of Corallina. Small plants of Bryopsis plumosa are also not uncommon here.

This classification and description is summarised in the appended table (Text-fig.3).

Ecological Unit	Principal factors determining its limits	Principal algae	Season of dominance or sub-dominance
I. Exposed micro-zone	Water level of pool (intolerance of submersion in pool)	Fucus spiralis F. vesiculosus var. evesiculosus Ceramium shuttleworthianum	Throughout year
II. Fringe micro-zone	Ability to withstand prolonged exposure & considerable variations of temperature & salinity of surface water	Cladophora rupestris Enteromorpha spp. Ulva lactuca var. rigida.	Throughout year (S.) Early spring (N.) March-May (N) Autumn-spring (N.)
III. Submerged micro-zone	Inability to withstand above conditions.		
(a) Open-pool micro-association	Light requirements		
(i) Silted micro-facies	Presence of silt covering	Rhodochorton floridulum Enteromorpha spp. Cladophora rupestris	November-March March-October Perennial community
(ii) Silt-free micro-facies	Water-flow (reduction of silting.) Wave damage	Ulva lactuca var. rigida Fucus sporelings Enteromorpha compressa Acrosiphonia centralis	Throughout year Throughout year Throughout year March-April
(b) Shade micro-association	Light and temperature extremes reduced.		
(i) Silted micro-facies	Presence of silt covering.	Rhodochorton floridulum Cladophora rupestris Polysiphonia nigrescens	November-April Perennial communities Pseudo-perennial community, winter & spring.
		Corallina officinalis	Perennial
(ii) Silt-free micro-facies	Water-flow. Raised above surrounding level. Hard surface	Lithothamnion lenormandii. Laurencia hybrida Dumontia incrassata	Perennial Pseudo-perennial Annual, spring.
(iii) Ledge micro-facies	Slope and orientation of ledges and bank.	Corallina officinalis Codium Polysiphonia urceolata	Perennial Pseudo-perennial, August-March Pseudo-perennial, winter and spring.

Text-fig.3. Table illustrating main features of bionomic divisions. (N.) = north bank, (S.) = south bank of pool.

3. Classification

The following list includes only species found growing within the pool: it does not deal with plants which occur only above the water level or those which are found as drift, even though some of the latter may survive for a considerable time entangled amongst the fronds of attached algae. It consists of 22 Chlorophyta, 14 Chrysophyta (Bacillariophyceae), 16 Phaeophyta, 7 Cyanophyta and 21 Rhodophyta, 80 species in all.

Apart from a few references by Aleem (1950) no list of Bacillariophyceae appears to have been published for St.Andrews. The present list contains only the species of major ecological importance or of very distinctive form, and is obviously far from being exhaustive. Thanks are due to Mr. R. Ross of the British Museum for checking or identifying several of the species. The distribution of the other groups has been extensively studied on the St.Andrews shore; Dunn (1939) summarises earlier published accounts and enumerates 184 species (excluding all listed as varieties or forms by Parke (1953)). The additional records of Blackler (1951) and several unpublished records give a total of 205 known species: 46 Chlorophyta, 59 Phaeophyta, 15 Cyanophyta, and 85 Rhodophyta.

It was not to be expected therefore that a survey of such a small area would produce many new records: those which have not so far been published are marked with an

asterisk. It is noteworthy however, that the algal population of the pool has at one time or another included very nearly a third of the species found in the entire area of the St.Andrews shore (about 7 miles of coast, including salt-marsh, mud, sand and rock), a proof if it were needed, of the diverse conditions obtaining within the pool.

It would be out of place to burden a relatively short list with a lengthy discussion of taxonomic and nomenclatural problems involved, but a few prefatory notes seem advisable. The nomenclature is largely in accordance with Parke (1953) with occasional revisions for which I am indebted to Miss L.M. Newton of the British Museum, but there are several differences in taxonomic arrangement, particularly in the Phaeophyta. In the Chlorophyta the Ulvales (Monostromataceae and Ulvaceae) are removed from the Ulotrichales (Hamel 1931, Kylin 1949, et al.), and the Chaetophorales placed after the Cladophorales (vide Fritsch 1935). The name Siphonales is illegitimate (Intern. Code Art. 27, Lanjouw 1952), and since Greville's original Ordo XIV Siphoneae (Greville 1830) included the genus Vaucheria, now referred to the Xanthophyceae (Chadefaud 1951) in the division Chrysophyta, it is better dropped. Greville does not distinguish families within his order, but it seems reasonable to take the family founded on the first genus listed by Greville (Codium) as the type family, and rename the order Codiales. The classification of the very incomplete list of

Bacillariophyceae follows primarily that used by Aleem (1950). The Phaeophyta are classified according to the system of Kylin (1933), but the Punctariales are included in the Dictyosiphonales (Papenfuss 1947) and the Scytosiphonaceae removed from the Punctariales (Dictyosiphonales) (Feldmann, 1949) and given their logical place in this system as an order of the Isogeneratae. The endings of the sub-classes Haplostichineae and Polystichineae have been altered to conform with Recommendation 26A(b) 1 and Article 27 of the International Code of Botanical Nomenclature (Lanjouw 1952). Lastly the Leathesiaceae have been separated from the Chordariaceae (Setchell & Gardner 1925, Fritsch 1945). The Cyanophyta are arranged according to Fritsch (1945) and the Rhodophyta to Drew (1951) and Kylin (1944).

4. List of Species

DIVISION: CHLOROPHYTA

CLASS: CHLOROPHYCEAE

ORDER: CHLOROCOCCALES

Family: CHLOROCOCCACEAE

Chlorochytrium cohnii Wright

Local and sporadic, but common to abundant where found, summer to winter, immersed in old tubes of tubicolous diatoms epiphytic on various algae in shade.

ORDER: ULOTRICHALES

Family: ULOTRICHACEAE

* Ulothrix pseudoflacca Wille var. minor Wille

Rare, spring, epiphytic on Ceramium rubrum, especially in the axils of the branches, in shallow parts of pool. 100 - 200 μ, cells 8.5 μ broad.

ORDER: ULVALES

Family: MONOSTROMATACEAE

Monostroma grevillei (Thur.) Wittr.

Frequent, February-May (- April, 1953), occasional to June, on bare rock or epiphytic on various algae, especially Cladophora rupestris, in all parts of the pool except deepest shade. To 4 cm. high.

Reproduction: Gametes produced, May-June.

Family: ULVACEAE

Enteromorpha compressa (L.) Grev. (Figs.28-30)

Frequent to abundant throughout year, epiphytic on various algae or attached to substratum, in all parts of pool, but poorly developed in shade. Ephemeral, with short, sparse winter growth developing slowly, and large, much-branched, abundant and rapidly developing plants in late spring/early summer. To 17 cm. (summer), 5 cm. (winter).

Reproduction: Gametes and zoospores liberated at irregular intervals throughout year. Generally bulk of population reproduces simultaneously, especially in calm, sunny weather.

Remarks: Very variable in size and form. Specimens of this

and E. intestinalis have been checked and the identification verified by Dr. Blíding, Sweden.

E. intestinalis (L) Link. (Fig.31)

Frequent to abundant March - June, occasional to September, on rock, shallow sunny parts of pool. To 30 cm.
Reproduction: Gametes and zoospores liberated under same conditions as for E. compressa.

E. linza (L.) J. Ag. (Fig.32)

Rare or occasional, irregularly throughout year, sometimes frequent in May and June, on rock in shallow, illuminated parts. To 25 cm. long and 5 cm. broad.
Reproduction: June.
Remarks: Summer plants are not unlike certain growth-forms of Ulva lactuca var, latissima.

E. prolifera(O.F.Müll.) J. Ag.

Frequent for most of year along northern fringe of pool Most typical growth in late spring. To 10 cm.
Reproduction: Similar to that of E. compressa.

Ulva lactuca L. var. rigida (Ag.) LeJol.

Abundant, February to April, until extreme neap tide exposures, thereafter common throughout rest of year, generally on bare rock, more rarely epiphytic on various alga, along northern fringe and in shallow parts.
Reproduction: At irregular intervals, generally under same conditions as for E. compressa.
Remarks: Plants are small, generally forming tight little rosettes.

U. lactuca L. var. latissima (L) D.C.

Occasional to frequent, spring, along northern fringe of pool.

Reproduction: As for var. rigida.

Remarks: Rather larger, paler, less compact plants than var. rigida. They can, however, only be separated with certainty from var. rigida by examination of the cross-section of the thallus.

ORDER: CLADOPHORALES

Family: CLADOPHORACEAE

Chaetomorpha melagonium (Web et Mohr) Kütz.

Rare, autumn, winter and early spring, on rock, usually in shelter of Cladophora or Polysiphonia communities

Remarks: Plants generally very stunted with small cells, e.g. 110 μ broad by 220 μ long, and covered with diatoms.

Rhizoclonium implexum (Dillw.) Kütz.

Abundant April-August and frequent at other times, entwined amongst various algae, especially Cladophora rupestris, in all parts of the pool except extreme shade. Cells 16-19 μ diam., 1⅓ - 2⅓ times as long as broad.

Cladophora rupestris (L.) Kütz. f. rupestris

Abundant throughout year in dense communities & fringing the pool, with scattered individual plants in all parts. Pseudo-perennial, to 5 cm.

Reproduction: Spores, spring and early summer.

Remarks: Often in very poor condition in summer and autumn,

submerged plants often heavily covered with epiphytic diatoms and Enteromorpha compressa and entwined with Rhizoclonium implexum. New growth prominent in spring.

C. sericea (Huds.) Kütz.

Rare, single specimen March, 1951. 4 cm.

Acrosiphonia centralis (Lyngb.) Kjellm.

Occasional in February, frequent in March and April, scattered throughout pool except in very shallow or shaded parts. To 7 cm.

Reproduction: Spores, March, April.

ORDER: CHAETOPHORALES

Family: CHAETOPHORACEAE

Sub-family: PROSTRATAE

Epicladia flustrae Rke.

Frequent throughout year, particularly in summer, on Dynamena pusilla (L.), in shade.

* Entocladia perforans (Huber) Levr.

Abundant March 1954, in tissues of Ceramium rubrum.

* Pringsheimiella scutata (Rke.) Marchew

Rare, February 1954, on Polysiphonia urceolata, vertical face of ledge.

* Ulvella lens Crn.

Rare, March 1954, on Polysiphonia nigrescens from deepest part of pool. 150 μ diam.

Family: TRENTEPOHLIACEAE

Gomontia polyrhiza (Lagerh.) Born. et Flah.

Occasional, summer, in periostracum of Littorina littorea (L.)

Reproduction: Sporangia, July.

Remarks: Probably more frequent but not often searched for.

Tellamia contorta Batt.

Frequent throughout year, in periostracum of Littorina littorea and L. littoralis.

Remarks: Approaches T. intricata Batt. in places: these two species seem doubtfully distinct.

ORDER: CODIALES (SIPHONALES)

Family: CAULERPACEAE

Bryopsis plumosa (Huds.) Ag. var. plumosa

Occasional throughout year but rare in early summer, in shade on rock, occasionally on bottom more usually on vertical or overhanging faces of ledges.

Reproduction: Probably entirely vegetative by creeping filaments.

Remarks: Plants very small with few erect thalli, often diatom-covered.

Family: CODIACEAE

* Codium tomentosum Stackh. (Figs.33 - 35)

Abundant July-March as spreading mosslike patches, occasional minute thalli sometimes formed October to March, present as creeping filaments for rest of year. Mainly developed on vertical faces of ledges. Poor growths also present amongst silt in shady parts.

Reproduction: Entirely vegetative by creeping filaments.

Remarks: See note 1 at end of list.

Family: PHYLLOSIPHONACEAE

* Ostreobium quekettii Born. et Flah

Rare, July, a few filaments in the periostracum of Littorina littorea.

DIVISION: CHRYSOPHYTA

CLASS: BACILLARIOPHYCEAE

ORDER: CENTRALES

SUB-ORDER: DISCINEAE

Family: MELOSIRACEAE

* Melosira moniliformis (O.F. Müll.) Ag.

Frequent throughout year, epiphytic on various algae, particularly in deep shady parts, in rather long chains.

* Podosira montagnei Kütz.

Common throughout year, epiphytic on various algae, particularly in shade, solitary or in short chains.

Family: COSCINODISCACEAE

Empty frustules not uncommon, presumably washed into pool: not further identified.

SUB-ORDER: BIDDULPHIINEAE.

Family: BIDDULPHIACEAE

* Biddulphia aurita (Lyngb.) Bréb.& God.

Occasional, winter, amongst basal parts of algae from deep shade.

ORDER: PENNALES

SUB-ORDER: FRAGILARIINEAE.

Family: FRAGILARIACEAE

* Synedra gaillonii (Bory) Ehrenb.

Occasional, winter, epiphytic on Polysiphonia nigrescens in shade.

* S. tabulata (Ag.) Kützg.

Frequent, winter and spring, on various algae, especially in deeper parts.

Family: TABELLARIACEAE

* Rhabdonema arcuatum (Lyngb.) Kützg.

Frequent, winter, in filaments on and amongst tufted algae, especially in deeper parts.

Grammatophora marina (Lyngb.) Kützg.

Frequent throughout year, on various algae, most commonly in deeper parts, in chains of varying length.

G. serpentina (Ralfs) Ehrenb.

Frequent throughout year on various algae in all parts of pool, in short chains.

Family: MERIDIONACEAE

* Licmophora paradoxa (Lyngb.) Ag.

Abundant throughout year, in short-stalked colonies epiphytic on various algae, particularly on Dumontia incrassata, often completely investing host.

Remarks: Frustules abundant in gut of Chironomid larva and Dinophilus taeniatus in February.

SUB-ORDER: ACHNANTHINEAE

* Achnanthes brevipes Ag.

Frequent, winter and spring, epiphytic on shade algae.

Cocconeis scutellum Ehrenb.

Abundant at all times and in all parts of the pool, on various algae, often so numerous as to form a complete cortication of the host.

SUB-ORDER: NAVICULINEAE

Family: CYMBELLACEAE

* Amphora exigua Greg.

Occasional, spring, epiphytic on shade algae.

Family: NAVICULACEAE

* Navicula grevillei (Ag.) Heib.

Abundant throughout year, especially in autumn and spring, in gelatinous tubes on rock and various algae, particularly on Cladophora rupestris.

Remarks: Identification is somewhat doubtful: other tubicolous species are almost certainly also present.

SUB-ORDER: NITZSCHIINEAE

Family: NITZSCHIACEAE

* Nitzschia closterium (Ehrenb.) W. Sm.

Occasional in winter, abundant in spring, amongst silt and algal filaments: not attached.

Remarks: This species often develops in quantity in cultures of pool material.

DIVISION: PHAEOPHYTA

CLASS: ISOGENERATAE

ORDER: ECTOCARPALES

Family: ECTOCARPACEAE

Pylaiella littoralis (L.) Kjellm.

Occasional, winter and spring, as small, poorly developed tufts on Cladophora rupestris and other algae. Turf 3.5 cm. long on Fucus pendant into pool from southern bank, autumn, 1952.

Reproduction: Unilocular sporangia, January - March.

Remarks: This species is abundant and well-developed in neighbouring pools of both higher and lower levels. Possibly severe wave action inhibits its further growth here.

Entonema parasiticum (Sauv.) Hamel (Streblonema parasiticum (Sauv.) De Toni)

Frequent in March, 1951, in axils of branches of Ceramium rubrum from deeper parts. Not found subsequently in that host, but fertile plants referred to this species abundant in tissues of Corallina officinalis, July, 1952.

Reproduction: Plurilocular sporangia, July, 1952.

Family: LITHODERMATACEAE

Petroderma maculiforme (Wollny) Kuck.

Rare, November, 1953, few small spots on Lithothamnion lenormandii, in deep shade. About 3 mm. diam.

Reproduction: Few unilocular sporangia.

ORDER: SPHACELARIALES

Family: SPHACELARIACEAE

Sphacelaris pennata (Huds.) Lyngb. var fusca (Huds.) comb.nov. Sphacelaria. (S. fusca Huds.) (Figs.36 - 39).

Abundant throughout year, especially in shade, on rock or more usually epiphytic on various algae, particularly Corallina officinalis and Cladophora rupestris. To 2.5 cm.
Reproduction: Unilocular sporangia rare, June 1951, occasional, December 1953. Propagules abundant, June - Sept., rare, Oct. - March.
Remarks: Non-epiphytic plants poorly developed and rarely bearing propagules. See note 2 at end of list concerning nomenclature and taxonomic status of this taxon.

Cladostephus spongiosus (Huds.) Ag.

Rare to frequent, of irregular occurrence throughout year, annual or semi-perennial, in all parts of pool except fringe, deep shade and ledges. Best developed amongst larger Chlorophyceae in deeper parts. To 5 cm.
Reproduction: Unilocular sporangia, August 1952 (one plant).
Remarks: Generally heavily covered with epiphytic diatoms and various Chlorophyceae.

ORDER: SCYTOSIPHONALES

Family: SCYTOSIPHONACEAE

Petalonia fascia (O.F. Müll.) Kuntze

Rare, irregularly October - March, on Lithothamnion lenormandii and on Balanus balanoides on ledge, southern side.

Pseudo-perennial, about 4 cm.

Reproduction: Plurilocular sporangia, March 1951

Scytosiphon lomentaria (Lyngb.) Endl.

Rare to frequent, irregularly July-April, most frequent October - December, on bare rock in various parts of pool, particularly along the top of ledges. To about 10 cm.

Reproduction: Plurilocular sporangia, winter.

CLASS: HETEROGENERATAE

SUB-CLASS: HAPLOSTICHOPHYCIDAE

ORDER: CHORDARIALES

Family: MYRIONEMATACEAE

Myrionema strangulans Grev.

Rare to frequent, summer, epiphytic on Ulva lactuca and Enteromorpha spp. in various parts of pool.

Reproduction: Unilocular sporangia, July, August.

Ulonema rhizophorum Fosl.

Rare, March and June, 1951, epiphytic on Dumontia incrassata. Not found subsequently.

Reproduction: Gametes liberated from unilocular sporangium, June.

Family: ELACHISTACEAE

Elachista fucicola (Vell.) Aresch.

Rare, August, 1952, on receptacles of Fucus spiralis pendant to surface of pool from southern side; not submerged for most of period of pool's exposure. To 8 mm.

Reproduction: Unilocular sporangia.

Family: LEATHESIACEAE

Leathesia difformis (L.) Aresch.

Rare, June - August, epiphytic on Corallina officinalis in deepest part. To 6 mm. diam. Minute plants, 150 - 250 μ diam., globular or encrusting, frequent on various filamentous hosts, deeper parts, March 1954.

Reproduction: Unilocular sporangia, 1 plant August, 1 plant March.

Remarks: The minute plants of spring may reproduce without further growth: they appear basally on filaments and rhizoids amongst the silt in the deepest part, whereas the summer plants develop on the more distal parts of Corallina.

SUB-CLASS: POLYSTICHOPHYCIDAE

ORDER: DICTYOSIPHONALES

Family: PUNCTARIACEAE

Punctaria plantaginea (Roth.) Grev. var. plantaginea.

Rare, March 1951, on rock in shade of Fucus plants near landward end. Not found subsequently. To about 6 cm.

Reproduction: Unilocular sporangia, March.

Family: ASPEROCOCCACEAE

Asperococcus fistulosus (Huds.) Hook. f. fistulosus

Abundant in summer, old plants occasional September - December, rare Feb., March 1954, on rock or epiphytic on Cladophora rupestris and Polysiphonia nigrescens in all parts except fringe and deep shade.

Reproduction: Unilocular sporangia, May - December.

ORDER: LAMINARIALES

Family: LAMINARIACEAE

Laminaria digitata (Huds.) Lamour.

Rare, young specimens in late summer disappearing by September, in deepest parts. To about 16 cm.

Reproduction: All plants examined sterile.

CLASS: CYCLOSPOREAE

ORDER: FUCALES

Family: FUCACEAE

Fucus spiralis L.

Abundant throughout year, fringing pool, particularly on shaded southern side. Many of the small Fucus plants within the pool, which rarely grow to more than 5 - 10 cm. appear to be this species.

Reproduction: Throughout year (fringe plants only).

Remarks: The small submerged plants are much overgrown with epiphytic Ceramium rubrum and Enteromorpha compressa.

F. vesiculosus L. var. vesiculosus

Rare, perennial, on southern side in shade, on fringe pendant into pool, one or two plants only.

Reproduction: October

Remarks: Air vesicles few and irregular.

F. vesiculosus L. var. evesiculosus Cotton

Occasional to frequent, perennial, on fringe of pool, particularly on southern side. May also be present amongst small stunted Fucus plants of pool.

Reproduction: Throughout year (fringe plants only).

F. serratus L.

Occasional or rare, perennial, small plants on fringe of pool with fronds submerged. Small Fucus plants within the pool may frequently be of this species, but their stunted and distorted development makes identification uncertain.

Reproduction: Antheridia, March, April 1951 (2 plants).

DIVISION: CYANOPHYTA

CLASS: CYANOPHYCEAE

ORDER: CHROOCOCCALES

Family: CHROOCOCCACEAE

* Aphanothece pallida (Kütz.) Rabenh.

Occasional, autumn, in small clumps on rock in centre.

ORDER: CHAMAESIPHONALES

Family: CHAMAESIPHONACEAE

Entophysalis conferta (Kütz.) Dr. et Daily

Occasional, winter and autumn, few small patches epiphytic on shade algae.

* E. crustacea (Ag.) Dr. et Daily

Abundant in host, July, in periostracum of Littorina littorea.

Reproduction: Conidangia not infrequent.

ORDER: NOSTOCALES

Family: RIVULARIACEAE

Calothrix pulvinata Born.et Flah. var. pulvinata

Frequent, irregularly throughout year, epiphytic on

various shade algae, particularly Polysiphonia nigrescens and Corallina officinalis.

Family: OSCILLATORIACEAE

Microcoleus chthonoplastes Gom.

Abundant throughout year, forming closely interwoven layer amongst grains of soft sandstone penetrating to about 1 mm. depth.

Remarks: Probably of some importance as an early colonist of newly bared rock surfaces.

* Oscillatoria subuliformis Gom.

Occasionally abundant in spring as early colonist of bared rock surfaces.

Spirulina subsalsa Gom. f. subsalsa

Locally frequent throughout year, amongst silt adhering to Sphacelaria and other algae.

DIVISION: RHODOPHYTA

CLASS: RHODOPHYCEAE

SUB-CLASS: FLORIDEOPHYCIDAE

ORDER: NEMALIONALES

Family: ACROCHAETIACEAE

Acrochaetium virgatulum (Harv.) J.G. Ag. f. secundatum (Lyngb.) Rosenv. (A. secundatum (Lyngb.) Näg.)

Rare, December (once) and spring, epiphytic on Ceramium rubrum and (once) on Sphacelaria. Plants minute, little developed.

Reproduction: Monospores (one plant), April 1953.

Remarks: This taxon is reduced to a form of A. virgatulum. As Rosenvinge (1909) has pointed out the two forms intergrade without perceptible distinction.

Rhodochorton floridulum (Dillw.) Näg.

Abundant throughout year in all parts of pool and surrounds, amongst silt and entangled amongst the basal parts of other algae.

Reproduction: Always sterile in the pool, reproducing by vegetative spread of filaments.

Remarks: I am indebted to Dr. K.M. Drew Baker for identifica: :tion of this plant. It forms a mossy carpet about 1 cm. thick over most of the bottom of the pool, most prominent in late winter/early spring. The cells are generally smaller and the tufts less luxuriant than in specimens from lower levels. They are often covered with diatoms, especially Cocconeis scutellum.

ORDER: GELIDIALES

Family: GELIDIACEAE

* Gelidium pulchellum (Turn.) Kütz.

Rare, pseudo-perennial, July - March as small tufts amongst silt in very restricted spots. Erect filaments to about 3 cm.

Reproduction: Always sterile, propagation by spread of horizontal filaments.

Remarks: No plants of this genus have been recorded with reproductive organs from the St.Andrews shore. Identification

is somewhat difficult in this genus; Dunn (1939) records G. crinale J. Ag., G. pusillum Le Jol. and G. corneum Lamour., but it seems probable that this is in fact the only local species. Specimens from St.Andrews have been referred with some doubt to this species by Dr. de Valera.

ORDER: CRYPTONEMIALES

Family: DUMONTIACEAE

Dumontia incrassata (O.F. Müll.) Lamour.

Frequent to common, November to July, on rock or epiphytic, especially on Corallina officinalis in shady parts.
Reproduction: Cystocarps and tetraspores, May - July.
Remarks: Young plants appear from November to January, developing very slowly to small plants of 2 - 5 cm. Growth is very rapid in spring; many plants die off without reproducing in late spring during neap tides, others lingering till July.

Family: POLYIDEACEAE

Polyides caprinus (Gunn.) Papenf.

Rare, a few small plants present irregularly from July to March amongst larger algae of the shade communities.
To 1.5 cm.
Reproduction: Always sterile, though larger and reproducing freely in neighbouring pools.

Family: CORALLINACEAE

* Melobesia minutula Fosl.

Rare, July 1952, epiphytic on Corallina officinalis,

deep shady part.

Remarks: Identification checked by Dr. S. Suneson, Sweden.

Lithothamnion lenormandii (Aresch.) Fosl. f. lenormandii

Abundant, perennial, encrusting rock, well-developed in deep shade and forming small sporadic patches in all parts of the pool where the rock surface is habitually exposed.

Remarks: A very important species in determining the nature of the substratum. It forms a hard, semi-permanent crust protecting the soft sandstone from further erosion.

Corallina officinalis L. f. officinalis.

Abundant, pseudo-perennial, upper parts tending to be killed off by exposure in late spring, though dead fronds may persist throughout summer. On shady faces of ledges and in deep shade, though dwarfed plants may survive in the open parts of the pool. To about 3 cm.

Reproduction: Cystocarps November 1950, tetraspores July 1952.

Remarks: An important community-forming plant, much overgrown with epiphytes, especially Sphacelaria pennata var. fusca (Fig.36).

ORDER: GIGARTINALES

Family: PHYLLOPHORACEAE

Phyllophora membranifolia (Good. et Woodw.) J. Ag.

Rare, January - March 1953, on rock in deep shade under overhanging southern bank. 2 cm.

Reproduction: All plants sterile.

Family: GIGARTINACEAE

Chondrus crispus (L.) Stackh. (Fig.42)

Occasional, perennial, few tufts in various parts, developing in deepest shade. Small plants elsewhere killed off in late spring. To 6 cm.

Reproduction: Tetraspores in spring: cystocarps late spring and autumn: neither are common.

ORDER: RHODYMENIALES

Family: CHAMPIACEAE

Lomentaria articulata (Huds.) Lyngb.

Rare in the pool, occasional on shady vertical southern face above water level. Within the pool small, stunted sporelings develop in winter and early spring in deep shady parts, epiphytic, usually on Cladophora rupestris, to about 1 cm.

Reproduction: Never reaches maturity in pool.

ORDER: CERAMIALES

Family: CERAMIACEAE

Callithamnion hookeri (Dillw.) Ag.

Occasional amongst fringe algae above water level, rare at or just below it on shady southern side.

Reproduction: Monospores, June 1951 (single plant found within pool).

* Ceramium deslongchampii Chauv. ex Duby

Single specimen, March 1951, on ledge in shade. 3 cm.

C. shuttleworthianum (Kützz.) comb.nov..

(C. acanthonotum Carm. ex J. Ag.)

Abundant amongst fringe algae above water level on both sides of pool, rare at or just below surface on shady southern side. To 2 cm.

Reproduction: Sterile when submerged.

Remarks: For a discussion of the nomenclature of this species see note 3 at the end of this list.

C. rubrum (Huds.) Ag. var. pedicellatum (D.C.) Duby.

Common for most of year, pseudo-perennial or ephemeral, mostly killed off by exposure in March or April, epiphytic on various algae, especially Polysiphonia nigrescens and Fucus spp. in all parts of the pool, more rarely forming small dense growths on bare rock and amongst silt. To 12 cm., usually about 5 cm.

Reproduction: Tetraspores and cystocarps irregularly throughout year, most abundant in September and March. Antheridia, August 1953.

Remarks: A species very sensitive to changes in environmental conditions, most readily killed by continued exposure to high temperatures, to a lesser extent by temperatures about 0°C. and to lowered salinity. Petersen's observation (1908, p.85) that antheridia are probably much scarcer in nature than tetraspores or cystocarps seems to be borne out here, as they have only been observed once, although often looked for.

Plants severely afflicted with galls are of frequent

occurrence: these are dealt with in more detail in note 4 at the end of this list.

Family: DELESSERIACEAE

Membranoptera alata (Huds.) Stackh.

Rare, two stunted specimens, August 1952, on rock in deep shade well under ledge. Larger 12 mm.

Reproduction: Both specimens were sterile.

Family: RHODOMELACEAE

Polysiphonia urceolata (Dillw.) Grev.

Occasional to common, pseudo-perennial, in shade amongst silt and other algae, especially on vertical faces of ledges, as prostrate creeping filaments in summer to early winter, forming small tufts in winter and spring to about 2.4 cm., though generally shorter.

Reproduction: Vegetatively by creeping filaments: tetraspores (one plant), April 1951.

Remarks: Plants of the pool are very small for this species.

P. brodiaei (Dillw.) Grev. ex Harv.

Rare, single plant, January 1953, epiphytic on Cladophora rupestris on top of central ledge, 2.2 cm.

Reproduction: Sterile.

P. nigrescens (Huds.) Grev. ex Harv. f. nigrescens.

Occasional to common, pseudo-perennial, fronds ceasing to grow and often dying back in late spring and regenerating in winter; on rock in shady parts, often in dense clump in deepest part.

Reproduction: Rare and spasmodic, tetraspores in spring.
Remarks: Much overgrown with diatoms, sedentary animals and various large epiphytes, especially Ceramium rubrum and (in summer) Enteromorpha compressa (Fig.46).

Rhodomela confervoides (Huds.) Silva

Rare, 2 specimens May and September 1953, on rock under shade of southern bank. To 5 cm.
Reproduction: Cystocarps, May.
Remarks: Abundant in open parts of nearby mid-tide pools.

Laurencia hybrida (D.C.) Lenorm. ex Duby.

Frequent to abundant, pseudo-perennial, forming small rosettes, solitary or in clumps, on rocks in partial shade, very rarely epiphytic on Corallina officinalis, in southern half of pool. Larger fronds mostly die back in April, though some persist to August. Only small rosettes of immature fronds are present in autumn and winter. To 3 cm.
Reproduction: Spermatangia in spring, tetraspores in summer and October, cystocarps in July. Records rather spasmodic, indicating that most plants usually fail to reach maturity.

Additional Notes

1. Codium tomentosum Stackh. (Fig.33)

The plant referred to this species was first observed on the St.Andrews shore by Dr. Blackler in November 1949, in a few pools on the Hind Rock. Since then it appears to have

spread somewhat and to have developed more vigorous growths, but a careful search has failed to reveal any trace of it in similar pools along several miles of the coast, so that at present it appears to be limited to some score of pools on the Hind Rock and a neighbouring ridge, all between M.T.L. and H.W.O.N.T. In all of these the position and type of growth is similar to that described, but in the deeper pools thalli are formed earlier (June, August), more regularly, and grow to as much as 5 cm. in height (Fig.34). The apical walls of the utricles (Fig.35) are invariably rounded, unthickened and without a mucro; utricles are on the average 420 μ long by 120 μ broad and have a length/breadth ratio of 3.61/1 (average of 100 utricles); hairs are very rarely formed and gametangia have so far never been observed.

At first the plant was referred to the little-known and rare C. amphibium Moore, described first from Roundstone, Galway (Harvey 1844), and since then reported from Clare Island (Cotton 1912), Cornwall (Tellam 1882) and the Isle of Man (Batters 1902). Examination of material in the herbarium of the British Museum showed that the Irish plants are rarely branched and of a rather brighter green and less firm texture. Notes from Dr. M.A. Wilson, Plymouth, and personal experience have shown that non-thalloid growths of Codium intermixed or not with very small thalli are much more widespread than is indicated in the literature, and from one locality to another show little constancy in type of

habitat, tide level and other characteristics. Thus the apical walls of the utricles may or may not be mucronate towards the tips of the thalli, and the latter may be generally unbranched or many times dichotomously branched, light or dark green, firm or flaccid.

Codium tomentosum Stackh. is extending its range in Scandinavia (Lund 1940), and enquiries have shown that this is also the case on the East coast of Britain. Batters (1902) does not report its presence between Durham and Peterhead. Batters (Berwick-on-Tweed 1890), G.W. Traill (Firth of Forth, Fife 1885, 1886 1889. 1890) and Greville (Firth of Forth, 1824), Dunn (St.Andrews, 1959) and Jack (Arbroath, 1890) apparently did not encounter it, and Brady (1860) reports it only amongst cast up algae on the Durham coast, where it was apparently rare (Harvey 1853), yet in addition to the St.Andrews record specimens have recently been reported from Berwick (Dr.Moss, Oct. 1949 in litt.) and at various points on the Northumberland coast (Mr. Lacey 1953 in litt.); these plants are generally small, though occasionally reported up to 15 cm. long, and near Aberdeen forms very similar to those of St.Andrews are reported to occur. It seems probable, therefore, that the St.Andrews plant is no more than an ecological variant induced by generally unfavourable conditions on the fringe of the expanding range of the species, its distinctiveness probably emphasised by isolation and purely vegetative mode of reproduction, and that similar

growths elsewhere may also be ecological variants of this or related species. The species C. amphibium, which has likewise never been found fertile, requires careful re-investigation.

2. Sphacelaria pennata (Huds.) Lyngb. var. fusca (Huds.) comb. nov. (Fig.36).

Conferva fusca Huds. Fl. Angl. p.486 (1762); Dillw. Brit. Conf. pl.95 (1808).

Sphacelaria fusca (Huds.) Ag. Spec. alg. 2: 34 (1828); Harv. Phyc. Brit. pl.149 (1846); Sauv. Journ. de Bot. 16: 393 (1902); Taylor Mar. Alg. N.E. Am. p.130 (1937).

Sphacelaria cirrosa (Roth) Ag. var. fusca (Huds.) Crn. Alg. mar. Finistere no.35 (1852) pro parte quoad syn. excl. spec. distrib.; Batt. Cat. Brit. Mar. Alg., J. Bot. 1902 (Suppl.): 39 (1902); Newton Handb. Brit. Seaw. p.190 (1931); Knight & Parke L.M.B.C. Mem. 30: 66, 111 (1931); all as "S. cirrhosa var. fusca" nom. illeg.

Sphacelaria cirrosa (Roth) Ag. f. fusca (Huds.) Holm & Batt. Ann. Bot. 5:81 (1890) as "S. cirrhosa f. fusca" nom. illeg.

The above is a list of the more important references to this taxon. As Sauvageau (1902) has indicated, its identity with the briefly described Conferva fusca of Hudson (1762) is, in the absence of authentic specimens, at least open to some doubt, Dillwyn's (1808) description and figures are somewhat conflicting, and the earliest indubitable

description is that furnished and illustrated by Harvey (1846).

The specimens known to Harvey came from the south coast of England, and early herbarium specimens from these localities in the British Museum and the Royal Botanic Gardens, Edinburgh, are indeed very distinctive: the colour is a rich dark brown, the branching is rather sparse and irregular, and the propagules are large, with straight, cylindrical arms and without an apical hair. Where a host is also represented it is nearly always Cladophora rupestris. It was mainly with specimens like these, from both sides of the English Channel, that Sauvageau also was familiar, when he reaffirmed the taxon's specific rank. It is, however, widespread on both the east and west coasts of Britain, growing on rock or on the smaller algae of the mid-tide pools, and is variable in degree and type of branching and in colour. The unilocular sporangia (Fig.39) (not seen by Sauvageau but figured by Dillwyn (1808) and mentioned by Knight & Parke (1951)) are similar to those of typical S. pennata and are, as in the typical variety, of relatively rare occurrence. The shape of the propagules (Figs.37 and 38) and the invariable lack of an apical hair seem alone to be constant features separating this taxon from acknowledged forms of S. pennata. In view of the known variability of the form of propagule in S. pennata distinction of a species on this basis alone seems unjustifiable, and the taxon is accordingly reduced to a variety of S. pennata

pending the discovery of further more reliable diagnostic characters.

The name S. pennata (Huds.) Lyngb. (Huds. 1762, p.486; Lyngb. 1819 p.105) is adopted in preference to S. cirrosa (Roth) Ag. (Roth 1800 p.314; Ag. 1824 p.164). The synonymy of both names is somewhat tangled: brief, inadequate descriptions and lack of type specimens, and the undoubted early confusion of this species with S. bipinnata (Kütz.) Sauv. and other related species add to the difficulties. A full discussion would be out of place here: suffice it to point out that S. cirrosa is in any case illegitimate, as Agardh in making the combination refers to Hudson's Conferva pennata as a synonym and should therefore have adopted the earlier specific epithet. The combination S. pennata var. fusca does not appear to have been made before.

In view of the confused state of our knowledge of the distribution of this genus in Britain a thorough revision of British material is certainly urgently required, as suggested by Parke (1953). A preliminary check of herbarium material suggests that var. fusca is the more common inter-tidal variety at least on eastern Scottish shores, though indubitable forms of var. pennata are preserved in the herbarium of the Royal Botanic Gardens, Edinburgh, from Kincraig, Earlsferry, Bute and Orkney. All material examined from the St.Andrews shore has so far proved referable to var. fusca.

Thanks are due to Miss L.M. Newton (British Museum) and

to Mr. D.M. Henderson (Royal Botanic Gardens, Edinburgh) for assistance in examining herbarium specimens in their charge, to Miss Newton for considerable assistance with the nomenclature and synonymy of both taxa, and to Dr. S.M. Lodge (Marine Biological Station, Port Erin) for Manx material of var. fusca.

3. Ceramium shuttleworthianum (Kütz.) comb. nov.

Ceramium ciliatum β acanthonotum Carm. ex Harv. in Hook. Brit. Fl. II p.336 (1833).

Acanthoceras shuttleworthianum Kütz. Linnaea 15: 739 (1841); Phyc. Gen. p.381 t. 46 f. IV (1843).

Ceramium acanthonotum (Carm. ex Harv.) J. Ag. In syst. alg. hod. advers. p.26 (1844).

The Code requires that when the rank of a taxon is changed, the correct epithet is the earliest legitimate one available in the new rank. In no case does a name or an epithet have priority outside its own rank (Art.70). Hence the combination Ceramium shuttleworthianum must be used when the taxon bearing the varietal name Ceramium ciliatum var. acanthonotum is considered a species. In his publication 'In systemata algarum hodierna adversaria' J. Agardh cites 'Kütz. tab. 46 IV !' which is a reference to a figure of Acanthoceras shuttleworthianum in Kützing's Phycologia Generalis (v.s.). Hence the combination Ceramium acanthonotum is illegitimate, since it was superfluous when

published.

The above information has been supplied by Miss L.M. Newton of the British Museum.

4. Galls on Ceramium rubrum (Huds.) Ag. (Figs.40 & 41).

From time to time throughout the year plants of Ceramium rubrum have been collected which were more or less heavily covered with galls. These plants have always been from the deeper, more sheltered parts of the pool, and often exist side by side with perfectly healthy and normal specimens. The galls may occur on any part and may be solitary and almost globular, resembling cystocarps in form and size (Fig.41) or conglomerated into formless swellings 0.5 or even 1.5 mm. long and about 0.5 mm. high, and may or may not be accompanied by a proliferation of smaller ramuli. In one interesting case of an infected tetrasporiferous plant the majority of the galls themselves contained masses of tetraspores which were clearly continuous with the nodal bands of tetraspores in the normal tissues (Fig.40). In no other case has any type of cell been observed other than that of the ordinary cells of Ceramium rubrum, and preparations have failed to show either copepods or other microscopic organisms within the galls.

The above considerations indicate that the galls are clearly not themselves parasitic plants, such as Choreocolax polysiphoniae Reinsch, which occurs locally on Polysiphonia

lanosa (L.) Tandy, or, as was at first suspected, C. tumidus Reinsch, an imperfectly known and rather dubious species described as parasitic on Ceramium (Reinsch 1875). Chemin (1932) investigated and described very similar galls which he encountered on a single specimen of Ceramium rubrum at Rotheneuf, and suggested that they might be caused by bacteria, as has been shown to be the case for galls occurring on certain other Rhodophyceae (Chemin 1931, et al.), although he could find no positive evidence of their presence. Certainly the localisation on individual plants indicates that they are not caused by mechanical damage alone, and the apparent absence of a causal agent lends support to a theory suggested by Dr. Pocock (in litt.) that in this case they are due to virus infection. If so this raises the interesting possibility that the disease may be transmitted by mites and small herbivorous crustaceans in the same way as certain virus diseases of terrestrial plants are spread by small animals.

IV. GENERAL OBSERVATIONS ON THE FLORA

1. Epiphytism

This is a particular type of plant inter-relationship which is of the highest importance amongst the pool flora, and so prevalent that it merits a section to itself. It is one of the features which make the charting of algal populations difficult, as in many cases the epiphytes are large enough to obscure the host completely and may themselves carry a further heavy crop of algae.

Rattray (1886a) was one of the earliest phycologists to make a close study of the nature and effects of algal epiphytism. He listed epiphytes and their hosts for the Firth of Forth area and examined the relationship between them, showing that in many cases the surface cells of the host were badly distorted by the epiphyte, and that the host plant exhibited greater rigidity and more stunted growth than the normal plant. He postulated a corresponding decrease in fertility of the host, but there seems no particular evidence to support this contention.

Lami (1934b) has suggested that each algal species creates a specific hydrogen ion concentration in its environment, and that this must limit possible epiphytic combinations of host and epiphyte. This might also account in part for the high specificity of certain epiphytic, and more particularly of endophytic species. Aleem (1950), referring

to diatoms, has suggested that algae may inhibit epiphytism by means of special secretions. He also notes that smooth-surfaced, foliose algae do not as a rule carry nearly as many epiphytes as those with branched, cylindrical thalli, and he classes the more common littoral algae in three groups according to the frequency of epiphytic diatoms on them. On the whole, however, physiological condition and growth form are more important than species in determining the extent to which a plant is liable to be overgrown with epiphytes. Chondrus crispus, for instance, is a plant which in its normal healthy condition in the shady part of the pool is rarely covered with epiphytes: the flat, smooth-fronds probably offer little hold to spores, without any special antibiotic secretion being required to inhibit their development. When growing amongst the dense Cladophora growth only a few centimetres further out in the pool, however, it becomes stunted, with much more divided fronds, and may be covered with quite a heavy growth of Enteromorpha compressa, Ceramium rubrum and other epiphytes. This is illustrated by the two specimens in fig.42. Cladophora rupestris is a plant particularly liable to become overgrown with epiphytes when growing submerged, but it seems probable that the correspondingly poorer growth of submerged plants in the pool is a cause rather than an effect of the heavy epiphytism. The plants of the community on the shallow side of the pool are relatively free of epiphytes until

severely damaged by prolonged neap tide emergence; shortly afterwards the dead and moribund distal cells may become completely covered by Enteromorpha sporelings (Fig.43), while healthy plants in deeper parts remain relatively unaffected. Rate of growth may also be important in inhibiting the lodgement of epiphytes, though this may be an effect of secretion and the smoothness of cell walls in young and active cells. Perennial plants are naturally more liable to settlement of epiphytes than short-lived ephemerals, and plants with a rigid cartilaginous or coralline structure rather than those with very delicate tissues (at least where the larger epiphytes are concerned). Thus Polysiphonia nigrescens and the small Fucus plants often carry very large epiphytes, particularly in the early autumn (Figs.44 - 46).

The effects of epiphytism are not easy to distinguish, since, as already indicated above, the hosts concerned are most frequently already somewhat unhealthy. The most obvious danger is that the vastly increased surface area renders both host and epiphyte liable to be torn away by wave action, and this is indeed the most frequent fate of the small Fucus plants. The occlusion of light may in some cases be harmful, but on the other hand the presence of an epiphytic covering may often be an advantage. Thus the virtual cortication of some algae, notably Rhodochorton floridulum and Polysiphonia nigrescens, by the diatom Cocconeis scutellum may protect the more delicate host tissues from damage by silt particles

in suspension and the attacks of various animals, and in the case of the larger epiphytes the host may be shielded from high temperatures or desiccation during times when the water level in the pool falls particularly low.

The epiphytes themselves may be roughly divided into obligatory, habitual, facultative and infrequent epiphytes. (1) The obligatory epiphytes are in general very small and from an ecological point view, relatively unimportant species, such as Pringsheimiella scutata and Melobesia minutula, often partly endophytic, as Entocladia perforans and Entonema parasiticum, and in many cases are specific to one or a small range of hosts, as Ulonema rhizophorum on Dumontia incrassata. (2) The habitual epiphytes normally grow on host plants, but may also occur on the rock. Rattray (1886c) noted that algae develop best in their usual habitat, which is well borne out by observations on this group of plants. Thus Ceramium rubrum growing on various hosts, particularly on Fucus spp., may develop into large, healthy plants up to 12 cm. long, and reproduces freely: the plants growing among the silt are short, much branched and more generally sterile. Similarly Sphacelaria pennata var. fusca growing on Cladophora rupestris or, more usually, on Corallina officinalis, forms dense tufts which in season produce abundant propagules; the plants on the substratum, however, are small, straggling growths which are rarely reproductive.

(3) The facultative epiphytes appear to grow equally well on either rock or other algae. They include several of the annual and ephemeral plants, such as Monostroma grevillei and Enteromorpha compressa.

(4) The infrequent epiphytes are species which normally grow attached to the rock but may sometimes develop, at least up to a certain stage, as epiphytes. They also illustrate Rattray's point: sporelings of Laurencia hybrida germinate on many of the shade plants but rarely develop beyond a few mm. at the most; Ulva lactuca var. rigida is sometimes found on Cladophora rupestris and other algae, but only as much smaller plants than normal. In this case, however, it may be early removal by wave action from an insecure foothold which prevents their further development.

Diatoms are exceedingly abundant as epiphytes, often multiplying so rapidly on the host as to cover its surface almost completely over a considerable area. This is particularly the case with Cocconeis scutellum, as already mentioned, and Licmophora paradoxa (Figs.47, 48). Their distribution on particular hosts is, however, most probably mainly influenced by depth, shade and temperature rather than by any specific host/epiphyte relationship.

The main advantages of an epiphytic habit for non-parasitic species appear to lie in the relative safety of the sporeling from browsing animals on bare rock and detritus feeders amongst silt, and a comparatively less crowded

environment with less danger of being cut off from illumination by silt, debris or the growth of neighbouring plants. The principal disadvantages are the difficulty of obtaining an initial footing, the danger of death or dislodgement of the host, and the increased risks of lethal desiccation during exposure.

2. Growth and Reproduction

The algae of the pool may be divided into abortive, sterile, vegetative and cyclic species, according to the extent of their growth and reproduction. (1) Abortive plants are those which can germinate in the pool but are killed at a very early stage. They are often difficult to identify with certainty, but include Lomentaria articulata and Laminaria digitata. (2) Sterile plants can exist in the pool for relatively long periods but cannot as a rule spread vegetatively or reproduce sexually or asexually, e.g. Polyides caprinus and Fucus spp. The population of both these groups must always be renewed from outside the pool, and to one or other belong most of the species recorded more rarely from the pool. (3) Vegetative plants may flourish quite well within the pool, but cannot normally under these conditions reproduce themselves by any means other than vegetative spread of filaments or rhizoids. Pseudo-perennial plants which regenerate fronds from a perennating basal part are included

here. Some plants in this category are not known to have any other method of reproduction on the St.Andrews shore, e.g. Codium and Gelidium pulchellum: others may reproduce by other means elsewhere on the shore, but never within the pool, for example Rhodochorton floridulum; still others may reproduce sexually or asexually in the pool under exceptionally favourable circumstances, but usually spread by filaments or a rhizoidal system, notably Polysiphonia nigrescens and P. urceolata. (4) Cyclic plants normally reproduce sexually or asexually within the pool, and have themselves been reproduced similarly. This includes all the ephemeral plants such as Ceramium rubrum and Enteromorpha compressa: annual plants are also included here, though part of their annual cycle may lie outside the pool.

These categories are, of course, somewhat arbitrary, and under differing conditions growth and reproduction of a plant or species may be encouraged or repressed. The reproduction of many specimens is prevented by premature decease during extreme neap tide exposures in the late spring or early summer. It will be seen that the vegetative plants provide the bulk of the permanent or semi-permanent vegetation of the pool; this type of growth and reproduction is especially suitable for tiding over periods of extremely adverse conditions, such as the pool plants and animals so frequently experience.

V. FAUNA OF THE POOL

The appended faunal list cannot be regarded as in any way complete or comprehensive. The animals have mainly been studied in relation to the algae, and hence emphasis has been placed on those from other habitats. Others have been recorded as and when seen and identified, but reluctance to disturb conditions in the pool over frequently has doubtless led to the overlooking of several species which burrow in the silt or retire into cracks or crevices, while many species have not been identified with sufficient certainty to warrant their inclusion in the list as individual species.

1. General Description of the Fauna

Owing to the shallow and exposed nature of the pool, animals of a length of more than about 1 cm. are relatively few in number and species. They include active forms (*Carcinus maenas*, *Leander squilla*, *Blennius pholas*) which take shelter during the day or on disturbance in the recesses of the deeply undercut southern side, the larger gastropods and chitons (*Littorina* spp., *Patella vulgata*, *Lepidochitona cinereus*) which are generally inactive during daylight exposure of the pool, sedentary forms which live on the underside of ledges (*Halichondria panicea*, *Ascidia conchilega*), in crevices (*Mytilus edulis*) or permanent burrows (*Venerupis saxatilis*), and on the basal parts of the longer-lived algae (*Leucosolenia botryoides*). Finally, there are the nemertines

and annelids which burrow actively in the silt and amongst the narrow crevices and densely entwined algal filaments and rhizoids, rarely emerging during daylight exposure of the pool (Cephalothrix linearis, Amphiporus lactifloreus, Eulalia viridis, Perinereis cultrifera, Audouinia tentaculata). To these may be added those which are washed in from lower levels (Actinia equina, Gibbula cineraria, Porcellana longicornis, Eupagurus bernhardhus) or from nearby rocks (Nucella lapillus), or cut off by the ebbing tide (Euthemisto compressa, Zoarces viviparus). Depending on their nature or condition these would normally leave the pool at an early opportunity or eke out a precarious existence in situ for a longer or shorter time before succumbing to unfavourable conditions.

The smaller animals have generally been obtained on and amongst algae brought into the laboratory for examination as fronds, whole plants, clumps, or the entire covering of a cleared area. They include the young of many species of which adults have seldom or never been encountered in the pool (Idotea sp., Nereis virens, Asterias rubens, etc.), seasonal species which vary greatly in abundance at different times of the year (Dinophilus taeniatus, Limapontia capitata), species which are more or less generally distributed in all parts of the pool (Skeneopsis planorbis, Fabricia sabella, Clunio marinus larvae, Rhombognathides seahami), and others which are more or less strictly localised to a particular

type of substratum, habitat or food plant (Balanus balanoides, Amphithoe rubricata, Idotea sp., Limapontia capitata, and many others). The various types of algal communities have different types of associated faunas, a few of which are dealt with in some detail elsewhere.

2. Synopsis of the Major Groups

The following brief summary of the representation of the various major groups in the pool fauna, together with observations concerning the more important species, is concluded by a list of all species recorded from the pool, drift specimens of sedentary forms or insects excepted). Of the 98 species recorded and identified, 35 are not included in the published faunal lists (McIntosh 1875, 1927), and nearly all of these 35 are new records for the St.Andrews shore. The system of classification used is based broadly on Hyman (1940): for the lesser taxonomic units the 6th edition of Parker & Haswell (1949) has been followed in part, the Plymouth Marine Fauna (Marine Biological Association 1931) and the Marine Fauna of the Isle of Man (Moore 1937) have been consulted, and various modern authorities drawn on for particular groups. Thanks are due to Dr. N.S. Jones (Port Erin) for some valuable suggestions as to the arrangement of the list.

The principal works consulted are listed under the various groups: the only general handbook used has been that of Eales (1950). Special thanks are due to the following for assistance in checking or identifying species as detailed in the faunal list (in which they are referred to by initials):- Mr. N. Tebble, British Museum (Foraminifera, Annelida): Dr. S. Prudhoe, British Museum (Platyhelminthes), Mrs. N.F. McMillan, Liverpool University (Mollusca), Mr. D.I.D. Howie, formerly Gatty Marine Laboratory (Annelida), Dr. G.M. Spooner, Plymouth Marine Laboratory (Amphipoda), Dr. J. Hobart, University College of North Wales, Bangor (Halacaridae), Dr. M.V. Lebour, Plymouth Marine Laboratory (Pycnogonida), amd to Dr. J.M. Dodd and Mr. J.L. Stevens, Gatty Marine Laboratory, for frequent advice and assistance.

PROTOZOA: Numerous species are present at all times, in the surface waters, amongst silt and bottom debris, and attached to algae in the shadier parts. Only a few of the more distinctive species have however, been identified.

FORAMINIFERA : (Cushman 1948): Gromia oviformis is occasionally frequent: others are not uncommon on Polysiphonia nigrescens and amongst the silt, but have not as a rule been identified.

CILIOPHORA (Hyman 1940, Mobius 1888): Abundant, mostly unidentified.

Vorticella marinum is particularly frequent on the larger

Rhodophyceae in the axils of the branches.

PORIFERA (Bowerbank 1865-82): The phylum is represented by only two species, both here about their upper tidal limit; Halichondria panicea, confined to the dark undersides of ledges, and Leucosolenia botryoides, particularly abundant epiphyte on the lower parts of Cladophora rupestris in the deeper parts of the pool, playing an important part in matting the fronds together to form a suitably sheltered environment for an abundant and varied microfauna.

COELENTERATA (Hincks 1868, Hyman 1940): Several hydrozoans are frequent to abundant on shady rock surfaces (Dynamena pumila) and amongst algal fronds (Coryne muscoides, Bougainvillea sp., Laomedea flexuosa). The group has not been studied in detail, and it is probable that one or two species have remained unidentified. The other classes have been represented only by a solitary specimen of Actinia equina resident in the pool for a few months. The high level, abundant silt and exposure to wave action probably combine to create an environment unfavourable for the anthozoa, few specimens of which occur in any of the nearby pools above M.L.W.O.N.T. level.

PLATYHELMINTHES (Gamble 1893), Meixner 1933): Several small species are abundant amongst the denser algal tufts, including Plagiostomum vittatum and Macrostomum hystrix, the only two

species identified with any certainty.

NEMERTINEA (McIntosh 1873): Many small specimens occur amongst the rhizoids and matted fronds of algae in the deeper parts of the pool but have not been further identified. Larger specimens, probably mainly of Cephalothrix linearis and Amphiporus lactifloreus, are not infrequent, burrowing in silt and crevices.

ASCHELMINTHES (Remane 1928): The heterogeneous classes of this phylum have not been studied in any detail. Rotifers are seen occasionally amongst the algal fronds. The sole representative of the Kinorhyncha present, the curious little Echinoderes dujardini, is not uncommon amongst the silt. Small nematodes are exceedingly abundant in all parts of the pool, wherever silt and detritus collect.

BRYOZOA (Hincks 1880, Marcus 1927). A few forms occur on algae growing in shade, particularly on their lower parts. Of these the commonest appears to be Bowerbankia imbricata.

MOLLUSCA (Alder & Hancock 1845-55, Forbes & Hanley 1853, Jeffreys 1862-69, Winckworth 1932, 1951): Molluscs are well represented in the pool. A few specimens of chiton (Lepidochitona cinereus) and limpet (Patella vulgata) occupy small clear areas of bare rock and probably have a considerable effect in retarding algal recolonisation, numerous small gastropods browse on and amongst the fronds of the living

algae (notably Skeneopsis planorbis and, amongst Cladophora rupestris, Limapontia capitata), while larger littorinids are usually congregated amongst drift algae lodged in the deeper parts. Small bivalves, Turtonia minuta and young Mytilus edulis, are abundant amongst the densely tufted algae, particularly Cladophora rupestris; larger bivalves are uncommo

SIPUNCULOIDEA: Phascolosoma minutum is the only representative of the phylum which occurs in the pool; it is confined to cracks and crevices in the rock and the basal parts of Corallina officinalis.

ANNELIDA (Fauvel 1923, 1927, McIntosh 1900-1923): The most numerous and striking annelids in the pool fauna are the small orange-red archiannelid Dinophilus taeniatus and the tubicolous chaetopod Fabricia sabella (Fig.50). The former is abundant, particularly amongst diatoms, from November to May, but very rare at other times. The latter is abundant at all times of the year and in all parts of the pool where there is a covering of silt or matted algal fronds or rhizoids, and would appear to perform an important function in binding and stabilising the silt. Spirorbis borealis is not uncommon on algae with rather rigid fronds growing in deeper parts of the pool. Perinereis cultrifera is apparently not uncommon, but lives in crevices and burrows, and adult specimens have only been seen in the open when spawning and

when the pool has been dried up. Most other annelids present are either very small species (Grubea pusilla, Nerilla antennata) or immature specimens of larger species, the adults of which do not appear to inhabit this tidal level, and are most frequently encountered in the deeper parts of the pool amongst the rhizoids and basal parts of algae and in the densely matted tufts of Sphacelaria pennata var. fusca.

ARTHROPODA: This phylum is represented in the pool fauna by numerous, varied and abundant species.

CRUSTACEA (Bate & Westwood 1863-8): Both ostracods and copepods are abundant at all times and occur in every part of the pool, particularly in the denser algal clumps, but none of the various species concerned has been identified with any certainty. The only cirriped present, Balanus balanoides, is confined to shallow parts where silt is not deposited and occasional emergence occurs, and is represented by a few small specimens with a high mortality rate in the summer months. The isopods (Sars 1899) are represented by juvenile specimens of Idotea, frequent amongst the fronds of Polysiphonia nigrescens and Ceramium rubrum in the deeper parts of the pool, but adults occur only at much lower levels on the shore, and it is difficult to determine the species of these juveniles. Amphipods (Chevreux & Fage 1925, Jones 1948, Sars 1895) are very numerous and important, and have been studied in some detail. The most common species are

Hyale nilssoni, an exceedingly active creature generally abundant amongst the Enteromorpha and other algae fringing the pool, both in and out of the water, Gammarus locusta, which is present mostly as juveniles in the shallower parts of the pool, Stenothoë monoculoides and juvenile specimens of Apherusa jurinei, usually associated amongst algal clumps in the deeper parts, and both abundant except in the summer months. The Stenothoë is exceedingly voracious, attacking dead or moribund animals with avidity in the laboratory. Gammarus locusta has been observed in the laboratory to do very considerable damage to a plant of Ceramium rubrum, breaking off the tips of the branches and devouring the cell contents, but it is not known to what extent this habit is a natural one. Of the Decapods (Bell 1853) no species is abundant: small specimens of Carcinus maenas are occasionally found at all times of the year and during the summer months up to half a dozen larger specimens, tucked well under the deeply undercut southern bank during the day. A few specimens of Leander squilla occur at irregular intervals, most constantly in the spring.

INSECTA: Numerous species of this class visit the pool, accidentally or otherwise, but probably only two species can legitimately be included in the fauna list. A few specimens of Lipura maritima can be seen on the surface of the water or on surrounding rocks and weed at any time of the year.

It is much more abundant, however, round higher level pools. The Chironomid Clunio marinus is a permanent inhabitant of the pool. The larvae can be found in all parts, but are most numerous amongst Cladophora rupestris in the deeper portions; they are naturally herbivorous.

ARACHNIDA: The class is represented by Halacarids (Andre 1946, Fountain 1953, Viets 1927, Newell 1947) and Pycnogonids (Bouvier 1923, Lebour 1945). The former are exceedingly abundant at all times; since this group has been relatively neglected in Britain rather more attention has been paid to it than its ecological importance perhaps deserves. The most abundant species, Rhombognathides seahami, is found in all parts of the pool and on surrounding weed at all times of the year, though in the deeper parts it tends to be replaced by Rhombognathus notops: both are herbivorous. The carnivorous Halacarus (Thalassarachna) basteri basteri and Copidognathus fabriciusi occur occasionally in the deeper parts, especially in spring, while the other species are relatively rare. Of the Pycnogonida, Anoplodactylus pygmaeus is not uncommon amongst Corallina officinalis.

ECHINODERMATA (Koehler 1921). The only natural representative of the phylum in the pool is the ophiuroid Amphipholis squamata, which is found occasionally amongst Corallina.

CHORDATA: The phylum is rather meagrely represented, the Tunicates, Ascidia conchilega and Sidnyum turbinatum, having been found only in late summer and autumn on the undersides of the overhanging southern bank. Of the fish (Jenkins 1925) small specimens of Blennius pholis are not uncommon from about May to December, with occasional larger specimens in the early summer.

3. Faunal List

Species marked * have not been recorded in the published faunal lists of St.Andrews (McIntosh 1885, 1927). Ch. = identification checked by: Id. = identified by. Identified personally unless otherwise stated.

PHYLUM: PROTOZOA

SUB-PHYLUM: PLASMODROMA

CLASS: MASTIGOPHORA

Several species encountered but not further identified.

CLASS: RHIZOPODA

ORDER: FORAMINIFERA

Family: GROMIIDAE

* Gromia oviformis Dujardin

Not uncommon in the deeper parts, attached to algae, rock or pebbles wedged under the ledges. 1.5-2 mm. diameter.

Family: MILIOLIDAE

Quinqueloculina sp.

Occasional amongst silt.

Triloculina sp.

Occasional amongst silt.

Family: TROCHAMMINIDAE

* Trochammina squamata Jones & Parker

Single specimen amongst Cladophora rupestris, deeper part of pool. (Id. N.T.)

Family: NONIONIDAE

* Elphidium crispum L.

Frequent amongst silt. (Id. N.T.)

Family: ROTALIIDAE

Rotalia beccarii (L.)

Common amongst silt. (Id. N.T.)

Family: ANOMALINIDAE

* Cibicides refulgens Montfort

Amongst silt. (Id. N.T.)

SUB-PHYLUM: CILIOPHORA

CLASS: CILIATA

SUB-CLASS: EUCILIATA

ORDER: SPIROTRICHA

SUB-ORDER: HETEROTRICHA

Family: FOLLICULINIDAE

* Folliculinopsis ampulla (Müller)

Occasional, winter and spring, on Polysiphonia nigrescens in the axils of the branches and in cultures of

material from the pool. For a more detailed description see note 1 following this list.

SUB-ORDER: HYPOTRICHA

? Stylonychia sp.

Ciliates doubtfully referred to this genus as frequent, occasionally abundant, amongst algal fronds, especially of Ceramium rubrum.

ORDER: PERITRICHA

Family: VORTICELLIDAE

* Vorticella marina Greeff

Frequent throughout the year, on various algae, especially on Ceramium rubrum and Polysiphonia nigrescens.

* Zoothamnion cienkowskii Wrzesniowski.

Single specimen with seven bells, on Ceramium rubrum, November 1953.

PHYLUM: PORIFERA

CLASS: CALCAREA

ORDER: HOMOCOELA

Family: HOMOCOELIDAE

Leucosolenia botryoides (Ellis & Solander)

Common at all times amongst tufted algae, particularly Cladophora rupestris, in the shadier parts. The spicules are common amongst the silt.

CLASS: DEMOSPONGIAE

SUB-CLASS: MONAXONIDA

ORDER: HALICHONDRINA

Family: AXINELLIDAE

Halichondria panicea (Pallas)

Very localised, perennial, on the underside of the central ledge and southern bank. Poorly developed and generally covered with small hydroid growths.

PHYLUM: COELENTERATA

CLASS: HYDROZOA

ORDER: HYDROIDA

SUB-ORDER: GYMNOBLASTEA

Family: CORYNIDAE

Coryne muscoides (L.)

Frequent in winter and spring, but encountered at all seasons, on the lower parts of Polysiphonia nigrescens, Corallina officinalis and Cladophora rupestris. Bearing abundant gonidia in May 1953. To about 3.0 cm.

Family: BOUGAINVILLIDAE

Bougainvillia sp.

Abundant at all times on the lower parts of Cladophora rupestris, Polysiphonia nigrescens and Corallina officinalis growing in shade.

Family: CLADONEMIDAE

* Eleutheria dichotoma Quatrefages (Hydroid Clavatella prolifera Hincks).

Single specimen, August 1952, amongst Cladophora

rupestris from the deeper part, containing ova in the brood pouch. The hydroid stage has not yet been recorded on the St.Andrews shore. (Ch. J.M.D.)

SUB-ORDER: CALYPTOBLASTEA

Family: CAMPANULARIIDAE

Laomedea flexuosa Hincks

Abundant in late summer and autumn, frequent at other times, in the deeper more sheltered parts, on rock, Corallina and Halichondria panicea.

Family: SERTULARIIDAE

Dynamena pumila (L.)

Localised in small patches on rock in shade, perennial. Occasionally grows on stunted Fucus plants. Usually with Epicladia flustrae growing on it.

CLASS: ANTHOZOA

SUB-CLASS: ZOANTHARIA

ORDER: ACTINIARIA

TRIBE: NYNANTHEAE

SUB-TRIBE: ENDOMYARIA

Family: ACTINIIDAE

Actinia equina L.

Single specimen, apparently washed into pool, October 1951 - March 1952, on ledge in deep corner of pool. Red. about 2 cm. diameter.

PHYLUM: PLATYHELMINTHES

CLASS: TURBELLARIA

ORDER: ACOELA

A small, delicate, leaf-shaped acoelan is frequent amongst silt and matted algal tufts. It is orange-brown, eyeless, and about 1 mm. long, but has not been further identified.

ORDER: MACROSTOMIDA

Family: MACROSTOMIDAE

* Macrostomum hystrix Oersted

Frequent in silt and amongst algal tufts. (Id. S.P.)

ORDER: ALLOEOCOELA

SUB-ORDER: CUMULATA

Family: PLAGIOSTOMIDAE

* Plagiostomum vittatum (Frey & Leuckart)

Occasional amongst silt and matted algal tufts, in deeper parts.

PHYLUM: NEMERTINEA

CLASS: NEMERTINI

SUB-CLASS: ANOPLA

ORDER: PALAEONEMERTINI

Family: CEPHALOTRICHIDAE

Cephalothrix linearis (Rathke) Oersted

Occasional amongst silt and matter algal fronds to 4.5 cm. Probably fairly common but not often seen or

identified with certainty.

ORDER: HETERONEMERTINI

Family: LINEIDAE

? Lineus longissimus (Gunnerus)

Rare, amongst silt, as juvenile specimens 1 - 10 cm. long. (Id. J.L.S.)

SUB-CLASS: ENOPLA

ORDER: HOPLONEMERTINI

Family: AMPHIPORIDAE

Amphiporus lactifloreus (Johnston)

Single specimen, amongst silt in shallow part of pool, November 1952, containing ova. Probably not uncommon but rarely emerging into open while pool is exposed.

PHYLUM: ASCHELMINTHES

CLASS: ROTIFERA

Occasional, amongst algal fronds, not further identified.

CLASS: KINORHYNCHA

ORDER: CYCLORHAGAE

SUB-ORDER: NOMOSOMATA

Family: ECHINODERIDAE

* Echinoderes dujardini Greeff

Frequent throughout year amongst silt (about 1 per sq. cm.). (Ch. N.T.)

CLASS: NEMATODA

Abundant at all times amongst silt, algal rhizoids and small particles of debris. Not further identified.

PHYLUM: BRYOZOA

CLASS: ECTOPROCTA

ORDER: GYMNOLAEMATA

SUB-ORDER: CHEILOSTOMATA

Family: MEMBRANIPORIDAE

Membranipora membranacea (L.)

Rare, March 1951, on Fucus specimen growing in deep shade.

SUB-ORDER: CTENOSTOMA

Family: VESICULARIIDAE

Bowerbankia imbricata (Adams)

Not uncommon on basal parts of tufted algae growing in shade.

PHYLUM: MOLLUSCA

CLASS: LORICATA

ORDER: CHITONIDA

Family: LEPIDOCHITONIDAE

Lepidochitona cinereus (L.)

Occasional, perennial, in small depressions on bare rock in various parts of pool and on a living Littorina littorea. Colour very variable. To 14 x 8 mm. (Ch. N.F.M.)

CLASS: GASTROPODA

SUB-CLASS: PROSOBRANCHIA

ORDER: ARCHAEOGASTROPODA

SUB-ORDER: PATELLACEAE

Family: PATELLIDAE

Patella vulgata L.

Occasional on open patches of hard rock in the pool and at the landward end where silt does not accumulate. Juvenile specimens, rarely more than 1 cm. in diameter.

SUB-ORDER: TROCHACEA

Family: TROCHIDAE

Gibbula cineraria (L.)

Rare. One or two specimens occasionally found in winter in shady corners of the pool, possibly washed in attached to drift algae.

ORDER: MESOGASTROPODA

SUB-ORDER: TAENIOGLOSSA

Family: LACUNIDAE

Littorina (Algaroda) littorea (L.)

Frequent. About a dozen adult or nearly full-grown specimens are always present, usually clustered in crevices under the banks and ledges while the pool is exposed, probably feeding mainly on the drift algae which collect in such places. Small specimens are frequent amongst algal fronds in all parts of the pool. (Juveniles id. N.F.M.)

Littorina (Littorivaga) saxatilis (Olivi)

Common around and in all parts of the pool. (Ch. N.F.M.)

Littorina (Neritoides) littoralis (L.)

Occasional, with L. littorea but more active during pool exposure.

Frequent colour variations.

Family: RISSOIDAE

Cingula (Onoba) semicostata (Montagu)

Frequent, amongst Corallina and on small cleared areas of rock. To 3 mm. long. (Ch. N.F.M.)

Family: SKENEOPSIDAE

Skeneopsis planorbis (Fabricius)

Abundant at all times on various algae in all parts and on small clear areas of bare rock. To 2 mm. diameter.

Family: OMALOGYRIDAE

* Omalogyra atomus (Philippi)

Frequent amongst various algae, particularly Cladophora rupestris.

SUB-ORDER: STENOGLOSSA

Family: MURICIDAE

Nucella lapillus (L.)

Rare. Single specimens from time to time in the deeper parts. Their stay is usually brief and their presence probably accidental. Specimens are often juvenile. Height of shell 12 mm.-30 mm.

SUB-CLASS: OPISTHOBRANCHIA

ORDER: ASCOGLOSSA

Family: STILIGERIDAE

* Hermaea dendritica (Alder & Hancock)

Rare. One, March 1952, on Ulva lactuca, 8 mm.; one, January 1954, on Codium, 14 mm. The latter is unusually large for this species. One, March 1954. (Ch. J.M.D.)

Family: LIMAPONTIIDAE

Limapontia capitata (O.F. Müller)

Abundant, April and May, occasional or rare throughout rest of year, nearly always on Cladophora rupestris in and around fringe of pool. Further details are given in note 2 at the end of this list.

CLASS: LAMELLIBRANCHIA

SUB-CLASS: PRIONODESMACEA

ORDER: FILIBRANCHIA

Family: MYTILIDAE

Mytilus edulis L.

Abundant at all times as juveniles to about 5 mm. in all parts, on rock and attached to various algae. Larger specimens occur rarely, lodged in crevices of bank and ledges.

SUB-CLASS: TELEODESMACEA

Family: ERYCINIDAE

Turtonia minuta (O. Fabricius)

Abundant, attached to various algae, notably

Cladophora rupestris and Polysiphonia nigrescens.

(Id. Dr. H.O. Bull)

Family: VENERIDAE

Venerupis pullastra (Montagu)

Rare, autumn, amongst silt in deeper part of pool, as very young specimens. (Id. N.F.M.)

* Venerupis saxatilis (Fleuriau)

Rare. One specimen, 3.2 x 2.0 cm., was exposed when part of the central ledge broke off during stormy weather, October 1952. Two other bivalves, probably of this species, are known to live in similar situations in other parts of the pool and have been identified provisionally by their projecting siphons.

PHYLUM: SIPUNCULIDEA

Family: SIPUNCULIDAE

Phascolosoma minutum Keferstein

Occasional amongst Corallina and Codium and in crevices under ledges. Specimen containing ova, 6 mm., September 1952.

PHYLUM: ANNELIDA

CLASS: ARCHIANNELIDA

Family: DINOPHILIDAE

Dinophilus taeniatus Harmer

Abundant October - May, absent or very rare at other times, in all parts of the pool, but especially amongst

diatom growths and the denser algal tufts. Further details are given in note 3 at the end of this list. (Id. N.T.)

Family: NERILLIDAE

* Nerilla antennata Schmidt

Not infrequent amongst silt and matted algae in shady parts. (Ch. N.T.)

CLASS: CHAETOPODA

ORDER: POLYCHAETA

Family: APHRODITIDAE

Harmothoë imbricata (L.)

Occasional, winter and spring, amongst algae of the shady ledges, mainly as small post-larval forms, e.g. with 10 chaetigerous segments, November 1951: 19 chaet. segm. January 1952. Adults may, however, be not uncommon but rarely seen, as several about 2 cm. long were exposed by the drying up of the pool in March 1953. Female with contained ova, April 1953. (Id. D.I.D.H., ch. N.T.)

Pholoë minuta (Fabricius)

Occasional, winter, amongst Corallina, small post-larval specimens. (Id. D.I.D.H., ch. N.T.)

Family: PHYLLODOCIDAE

Eulalia bilineata (Johnston)

Single specimen, March 1953, driven from crevice in central ledge by drying up of pool. 3.5 cm. long.

Eulalia viridis (O.F. Müller)

Occasional in silt and matted algal clumps, both post-larval and adult specimens.

Eteone picta Quatrefages

Single post-larval specimen, 3.5 mm., May 1953, in silt from deep part. (Id. D.I.D.H.)

Family: HESIONIDAE

Kefersteinia cirrata (Keferstein)

Single specimen, August 1952, amongst Corallina. 4 mm. (Id. D.I.D.H.)

Family: SYLLIDAE

Syllis armillaris (Müller) Oersted

Single specimen, 14 mm. November 1951, amongst Corallina. (Ch. N.T.)

* Grubea pusilla Dujardin

Not infrequent amongst Corallina, Codium and silt in the deeper parts of the pool. 2 mm. long. (Ch. D.I.D.H.)

Family: NEREIDAE

Nereis diversicolor O.F. Müller

Occasional small specimens amongst Corallina.

Nereis virens Sars.

Single post-larval specimen, 4 mm., August 1952, amongst Corallina. (Id. D.I.D.H.)

Perinereis cultrifera (Grube)

Occasional in silt and crannies, juveniles and adults. In May 1953, about 12 adults in heteronereid state were seen

swarming on surface at 09.00 hrs. just before tide entered pool. (Ch. J.M.D.)

Family: SPHAERODORIDAE

Ephesia gracilis Rathke

Single specimen, 1.2 cm., April 1953, amongst Corallina. (Id. D.I.D.H.)

Family: SPIONIDAE

Scolecolepis fuliginosa (Quatrefages)

Occasional, winter and spring, amongst Corallina. Immature specimens to 4 mm. long. (Id. D.I.D.H.)

Family: CIRRATULIDAE

Audouinia tentaculata (Montagu)

Single specimen, captured at night by flashlight, November 1953, emerging from burrow in silt. Believed to be frequent and the main cause of the numerous large slime trails in pool, which always lead to a burrow. Liberated motile sperms and morulae in laboratory.

Family: SABELLIDAE

Fabricia sabella Ehrenberg (Fig.50)

Very abundant at all times and in all parts, particularly amongst silt and algal tufts, and especially amongst Codium and Rhodochorton, in small vertical tubes of silt particles. Serves an important function as a silt-binding agent. (Id. D.I.D.H.)

Family: SERPULIDAE

Pomatoceros triqueter (L.)

Occasional, on stunted Fucus plant in shade, on small stones wedged under the central ledge, and on rock below the overhanging southern bank.

Spirorbis borealis Daudin

Frequent, on small stones wedged under ledges and on cartilaginous algae in the deeper parts of the pool, i.e. on Fucus, Chondrus crispus and the basal parts of Polysiphonia nigrescens.

PHYLUM: ARTHROPODA

CLASS: CRUSTACEA

SUB-CLASS: OSTRACODA

Several species are abundant in all parts of the pool amongst silt and algal fronds, but have not been further identified.

SUB-CLASS: COPEPODA

Many species are abundant amongst silt and algal fronds but have not been further identified.

SUB-CLASS: CIRRIPEDIA

ORDER: THORACICA

Family: BALANIDAE

Balanus balanoides (L.)

Uncommon, on rock in isolated patches where silt does not accumulate and occasional emergence occurs. Many minute specimens in May, but few survive for long. Rarely active during exposure of the pool.

SUB-CLASS: MALACOSTRACA

ORDER: TANAIDACEA

Family: TANAIDAE

* Tanais cavolini Milne-Edwards

Occasional amongst algal fronds in various parts of the pool and amongst fringing algae. Usually juveniles. To 4 mm.

ORDER: ISOPODA

SUB-ORDER: VALVIFERA

Family: IDOTEIDAE

Idotea viridis (Slabber)

Single specimen 1.4 cm. long, December 1953, on Ulva lactuca.

Idotea sp.

Frequent except in summer amongst algal fronds, particularly of Polysiphonia nigrescens and Ceramium rubrum, as small juvenile specimens up to about 5 mm. length, usually red-brown, too immature for positive identification.

ORDER: AMPHIPODA

SUB-ORDER: GAMMARIDEA

Family: STENOTHOIDAE

Stenothoë monoculoides (Montagu)

Abundant, except following drying up of pool, amongst algal fronds in the deeper parts. With ova and young, July and August.

Family: CALLIOPIIDAE

* Calliopius crenulatus Chevreux & Fage

Occasional, winter and spring, amongst algae in the deeper parts. (Ch. G.M.S.)

Calliopius laeviusculus (Krŏyer)

Single male, 15 mm., March 1952, amongst Enteromorpha.

* Apherusa jurinei (Milne-Edwards)

Common, except following drying up of pool, amongst algal fronds, mostly as juveniles. Adults occasional, females with ova encountered May, September and November. This is the southern and not the Norwegian form (vide Chevreux & Fage, 1925, p.182).

Family: GAMMARIDAE

Gammarus locusta G.O. Sars sens. str.

Occasional-frequent, in all parts of pool, swimming freely or amongst algae. Juveniles most frequently captured but adults not rare.

Family: DEXAMINIDAE

Dexamine spinosa (Montagu)

Single specimen, female, 3 mm., August 1952, amongst Corallina.

* Dexamine thea Boeck

Single specimen, September 1952, amongst algae in deepest part of pool.

Family: TALITRIDAE

Hyale nilssoni (Rathke)

Abundant around edges of pool amongst algae both in and out of water. Very active. Females carrying ova frequent during summer months.

Family: AORIDAE

Aora typica Kröyer

Single juvenile specimen, 3 mm., February 1953, amongst Sphacelaria pennata var. fusca.

Family: AMPHITHOIDAE

Amphithoë rubricata (Montagu)

Occasional, generally juvenile specimens, forming nests of algal detritus attached to algae in the deeper parts of the pool.

Family: COROPHIIDAE

* Corophium bonelli (Milne-Edwards)

Occasional amongst silt and the matted basal filaments of Codium and Rhodochorton. To 2 mm. (Ch. G.M.S.)

SUB-ORDER: HYPERIIDEA

Family: HYPERIIDAE

Themisto compressa Goes

Single female, 17 mm., with young about to hatch, February 1952, swimming freely in pool. (Id. J.L.S., ch. G.M.S.

ORDER: DECAPODA

SUB-ORDER: NATANTIA

TRIBE: CARIDEA

Family: PALAEMONIDAE

Leander squilla (L.)

Occasional, often absent for long periods, especially in winter, returning in spring but rarely more than six present in the pool at one time. During exposure of the pool they tend to keep to the shelter of the overhanging bank. To about 5 cm. long.

SUB-ORDER: REPTANTIA

TRIBE: ANOMURA

Family: PORCELLANIDAE

Porcellana longicornis (L.)

Single specimen, March 1951, in good condition but obviously washed in from much lower levels.

TRIBE: PAGURIDEA

Family: PAGURIDAE

Eupagurus bernhardus (L.)

Occasional, actively crawling about in all parts of the pool, both by day and night. Probably washed into pool by rough weather, but individual specimens may stay in pool for many days, possibly weeks.

TRIBE: BRACHYURA

Family: PORTUNIDAE

Carcinus maenas (Pennant)

Occasional. Small specimens, 1 cm. or less in width of carapace, may be found now and again in any part of the pool and at any time of the year. Larger specimens, to about 7 cm. in width of carapace, move into the pool about

May and leave it by September. During exposure of the pool by day they remain in the deepest recesses of the overhanging bank and ledges but become active when dusk falls.

Family: MAIDAE

Hyas araneus (L.)

Single specimen with damaged rostrum, carapace 4 cm. broad, January 1951, clearly washed into pool from lower level (or dropped by sea-bird).

CLASS: INSECTA

SUB-CLASS: APTERYGOTA

ORDER: COLLEMBOLA

* Lipura maritima Guérin

Occasional, one or two at a time, on the surface of the pool or the surrounding rock, at any time of year.

SUB-CLASS: PTERYGOTA

DIVISION: ENDOPTERYGOTA

ORDER: DIPTERA

Family: CHIRONOMIDAE

* Clunio marinus Haliday

Larvae abundant throughout year amongst algal tufts in all parts, browsing on the fronds. Pupate and hatch on calm, sunny days in succession of broods from March to October, majority of late brood wintering as larvae. For fuller details see note 4 at the end of this list.

CLASS: ARACHNIDA

SUB-CLASS: ARACHNOIDEA

ORDER: ACARINA

Family: HALACARIDAE

(For a comparison with general distribution on the Hind Rock see note 5 at the end of this list).

Sub-family: RHOMBOGNATHINAE

* Rhombognathus notops (Gosse)

Not infrequent on various algae in the deeper parts of the pool. (Ch. J.H.)

* Rhombognathides pascens (Lohmann)

Single specimen, December 1953, amongst Codium. May be more frequent but difficult to separate from Rhombognathus seahami except on close examination.

* Rhombognathides seahami (Hodge)

Very abundant amongst algae throughout pool and on surrounding rocks. (Ch. J.H.)

* Rhombognathides mucronatus (Viets)

Single specimen, December 1953, amongst Corallina and Codium. Probably more frequent, but not readily separated from R. seahami.

* Metarhombognathus armatus armatus (Lohmann)

Single specimen, April 1953, amongst Cladophora rupestris in deep part. (Ch. J.H.)

Sub-family: HALACARINAE

* Halacarus (Thalassarachna) basteri basteri (Johnston)

Frequent amongst basal parts of algae in deeper parts of pool. Occasional elsewhere. (Ch. J.H.)

* Copidognathus fabriciusi (Lohmann)

Occasional-frequent, spring and summer, amongst algal clumps and basal silt in the deeper parts. (Ch. J.H.)

* Copidognathus oculatus Lohmann

Occasional, amongst algae in the deeper parts. (Ch.J.H.)

Sub-family: SIMOGNATHINAE

* Simognathus minutus (Hodge)

Single specimen, April 1953, amongst Sphacelaria pennata var. fusca. (Ch. J.H.)

SUB-CLASS: PYCNOGONIDA

ORDER: NYMPHONOMORPHA

Family: NYMPHONIDAE

* Nymphon brevirostris Hodge

Single specimen, November 1951, amongst Corallina. (Ch. M.V.L.)

Family: PHOXICHILIDIIDAE

* Anoplodactylus pygmaeus (Hodge)

Occasional amongst Corallina. Female with contained ova, August 1952; specimen which liberated live young in laboratory, July 1952. (Ch. M.V.L.)

ORDER: ASCORHYNCHOMORPHA

Family: AMMOTHEIDAE

Ammothea sp.

Several juveniles, August 1952, amongst Corallina. Possibly A. echinata Hodge or A. laevis Hodge, fide M.V.L.

PHYLUM: ECHINODERMATA

SUB-PHYLUM: ELEUTHEROZOA

CLASS: ASTEROIDEA

ORDER: CRYPTOZONIA

Family: ASTERIIDAE

Asterias rubens L.

Single specimen, 5 cm. diameter, May 1953, clinging to underside of overhanging bank, probably washed in by rough seas. Early post-larval stage, 1 mm. diam. July 1953, amongst Cladophora rupestris.

Note:- At this time similar stages were abundant amongst algae from lower levels.

CLASS: OPHIUROIDEA

ORDER: ZYGOPHIURAE

Family: AMPHIURIDAE

Amphipholis squamata (Delle Chiaje)

Occasional amongst Corallina.

PHYLUM: CHORDATA

SUB-PHYLUM: UROCHORDA

CLASS: ASCIDIACEA

Family: ASCIDIIDAE

Ascidia conchilega O.F. Müller

Rare. Few specimens, September 1953, adhering to overhanging bank. One specimen measured 2.1 cm. long, 1.4 cm. broad, 0.5 cm. high.

Family: SYNOICIDAE

* Sidnyum turbinatum Savigny

Rare. Very restricted patch, July 1953, hanging from roof of overhanging bank. To 12 mm. high.

SUB-PHYLUM: GNATHOSTOMATA

CLASS: ACTINOPTERYGII

SUB-CLASS: NEOPTERYGII

ORDER: PERCOMORPHI

Family: BLENNIIDAE

Blennius pholis L.

Occasional. Large specimens (to 10 cm.) generally present in shelter of overhanging bank and ledges during late spring and summer. To about 12 small specimens (2 - 5 cm.) generally present and active in all parts of pool from May to December.

Zoarces viviparus L.

Single young specimen, 5 cm. long, April 1952, under central ledge.

Additional Notes

1. Folliculinopsis ampulla (Müller)

The validity of this specimen has been questioned by Das (1949, p.386). Nevertheless specimens examined have had a simple case, short-necked with a slight lip and no grooves or other markings, a macronucleus of about 14-15 beads, each with a nucleolus, and two short, rounded peristomial

lobes, a combination of features which seems to place them in this species.

2. Limapontia capitata (O.F. Müller)

This species is markedly seasonal in its abundance, and was studied rather closely in an attempt to discover the factors controlling this periodicity. The ecology of the species has been dealt with in some detail by McMillan (1947), and the present study confirms that author's findings on many points.

A few specimens can generally be found in the pool about mid-April: numbers increase very rapidly indeed, and by May they are abundant, occurring in all parts of the pool but particularly associated with Cladophora rupestris on which they feed almost exclusively. Under adverse neap tide conditions in May they become greatly reduced in numbers, the Cladophora also being severely affected, and specimens are rarely found in autumn and winter. Breeding continues, however, throughout late spring and summer, juvenile specimens being found as late as the end of July. The controlling factor appears to be temperature, for scattered specimens were found throughout the mild winter of 1953-54, yet not during the more severe winter of 1952-53. McMillan (loc.cit.) found spawn only once in the pools which she studied: although the animals mate and spawn very readily in the laboratory, this does not seem to occur to nearly the same extent naturally. Spawn has, however, been found from time to time,

characteristic sausage-shaped masses attached to the axils of the lower branches of Cladophora rupestris, mainly in the shallower parts of the pool. Animals kept in the laboratory mated readily when brought together. They did not appear able to sense each other's presence until brought into actual physical contact, and possibly this occurs less readily under natural conditions. Small specimens mate freely and frequently: those which were segregated from an early stage grew to be much larger (about 5 mm. instead of the more usual 2 mm.), though conditions were otherwise similar. The age at which mating first occurs may therefore possibly explain the wide disparity in the sizes of mature individuals found under natural conditions.

Two large specimens thus segregated were brought together and then again separated. Both began depositing spawn within 3 days. One deposited in all 11 spawn-masses over a period of 16 days, each containing 150-200 ova, altogether 1,729 ova, all of which were fertile except for a small final batch of 71. The ova developed into free-swimming veligers within about 14 days. Attempts to rear the veligers were all unsuccessful: although they remained alive for as long as a fortnight only one out of many hundreds succeeded in metamorphosing.

In the laboratory the animals showed a preference for Acrosiphonia centralis over Cladophora rupestris and for young growth rather than for old. They also took

Codium and Bryopsis, and indeed seem prepared to accept any Cladophorales and Codiales offered. However, they appeared to spurn all other algae made available to them (Enteromorpha spp., Ulva lactuca, Sphacelaria pennata var. fusca and Polysiphonia urceolata), as observed by McMillan (loc.cit.). Their occasional presence on various other algae is therefore probably largely accidental. Even the Cladophora, however, does not seem greatly affected by their depredations, though these may possibly be more serious where very young Cladophora sporelings are concerned.

3. Dinophilus taeniatus Harmer

This is another species showing pronounced seasonal fluctuation in abundance. In this case, however, the species is primarily a winter inhabitant of the pool. One or two specimens can be found towards the end of September or beginning of October, and thenceforward numbers increase very rapidly. From November to March specimens are exceedingly abundant, particularly amongst diatoms and smaller algae in the deeper parts. Numbers begin to decline in April or May, especially in the shallower parts, adults being generally rare in May, while none has ever been found, despite careful search, from June to mid-September. A similar periodicity for the species is recorded from Plymouth (abundant November-April, rare or absent at other times) (Marine Biological Association 1931). In the laboratory

they breed freely and are easily kept during the winter, but die rather readily in the late spring, presumably killed by the rise in temperature. Ova are not infrequently encountered under natural conditions throughout the period during which the animal is present, as small clumps of 6-10 ova in a gelatinous envelope attached to the lower parts of algae, particularly Cladophora rupestris. The young hatch without metamorphosis about a fortnight after the ova are deposited (under laboratory conditions). They resemble the adult animal but are paler, more regularly tapered posteriorly, and swim more actively than the adults, which prefer to glide over the surface of the substratum.

The animals appear to be detritus feeders, at least in part, but frustules of various species of diatom have been seen in the gut of several specimens, and it is possible that they play a significant part in reducing the number of diatoms present in the autumn.

4. Clunio marinus Haliday

The larvae of this chironomid are abundant in all parts of the pool throughout the year amongst silt and algal tufts. They are at least normally herbivorous, but are not restricted to any particular species or even class of alga, though perhaps most numerous amongst Cladophora rupestris. In the laboratory they have been reared on a diet of liver powder alone, but the growth rate was slow, mortality was high and

very few metamorphosed successfully.

Metamorphosis appears to be largely controlled by temperature, though it is possible that a light stimulus is also required. Very occasionally an imago is formed during March on bright calm days when the pool temperature may reach about 8°C, and in the laboratory metamorphosis to the pupa stage has been obtained in January, but as a rule a minimum water temperature of about 10°C seems necessary. About April metamorphosis, at least of winged specimens, begins to occur more frequently. Pupation must occupy a very short time, as pupae have so rarely been found in the pool. The pupa rises to the surface, and within about 30 secs. the imago is on the wing. The rate of emergence of the imago on calm, sunny, summer days is about 7 per hour per sq. metre of surface area. The metamorphosis of the wingless female has not been observed, but presumably occurs under rather different conditions, perhaps only in the evening, as they were numerous on the surface of the pool at 1730 hours on a May evening, each surrounded by a number of males. Eggs are deposited in a mucilaginous string about 1 cm. long and containing about 130 white, fusiform ova, 280 x 100 μ, which hatch out in seven days under laboratory conditions as minute larvae about 0.4 mm. long. In the pool these grow rapidly, and a succession of generations is maintained throughout the summer. The numbers

metamorphosing diminish during the autumn until by the end of October they are very small indeed, the majority of the autumn larvae deferring metamorphosis until the late spring of the following year.

The laboratory-bred specimens were definitely referable to this species. It is possible, however, indeed probable, that larvae of other marine chironomids are also present, but have not as yet been identified.

5. Distribution of Halacaridae on the Hind Rock

Since the St.Andrews faunal records, published and unpublished, contained no references to this rather neglected group of animals, it was felt that a rather wider knowledge of their local distribution would be required in order to understand more clearly their distribution within the pool. Accordingly samples of algae and silt from various levels and types of habitat on the Hind Rock were examined from time to time and the mite population identified and counted. In general these counts have shown a clear preponderance of one or other species of rhombognathid in a particular habitat, but the samples have been rather small, and it may well be that distribution, even in this restricted area, is not so clear-cut as the results summarised in the accompanying table (Text-fig.4) indicate.

Species	Most characteristic Habitat	
	(a) in the pool	(b) on the Hind Rock
Rhombognathus notops (Gosse)	Deeper parts, freq.	M.T.pools, rather deep
R.magnirostris var. lionyx Trt.	-	M.T., deep pool, 1 spec., Nov. 1953
Rhombognathides pascens (Lohm.)	Deep, shady part, 1 spec., Dec.1953.	M.T. L.W.O.S.T.on Rhodophyta, deep pools (M.T.), widespread at lower levels, June 1953.
R.seahami (Hodge)	All parts, fewer in deep shade, abundant.	H.W.O.S.T. M.T. on algae in shallow pools, on rock in shade.
R.mucronatus (Viets)	Deep, shady part, 1 spec., Dec.1953.	-
Metarhombognathus armatus armatus (Lohm.)	Deep, shady part, 1 spec.,April 1952.	H.W.N.T.amongst algae on exposed rock, freq., April 1954
Halacarus basteri basteri (Johnston)	Deeper parts, freq.	H.W.O.S.T.downward amongst algae on rocks in shade & in pools, freq.
Copidognathus fabriciusi (Lohm.)	Deeper parts, freq.	M.T.deep pools, occ. Nov.1953, freq. May 1953.
C.oculatus Lohm.	Deeper parts, occ.	M.T.deep pools,
Simognathus minutus (Hodge)	Deep, shady part, 1 spec., Apr.1953	Not found elsewhere, probably generally infralittoral.

Text-fig.4. Distribution of Halacaridae on the Hind Rock.

VI. INTER-RELATIONS OF FLORA, FAUNA AND ENVIRONMENT

1. Plant and Animal Communities

It is now possible to consider in more detail the relationships between the plants and animals described in the species lists. In addition to examination of individual algal fragments and whole specimens, small clumps of algae and rock scrapings, information about the composition of particular communities has been obtained by complete removal to the rock underneath of everything within a wire square, of 5 cm. side, laid carefully over a sample of the community to be studied. The very soft nature of the rock makes this a comparatively simple operation, but the very slow rate of recolonisation made it undesirable as a regular practice.

The material was kept in petri dishes in a cool place: the larger animals were immediately removed and measured, detailed examination, frond by frond, was carried out as quickly as possible, and the silt and debris also subjected to careful scrutiny under a binocular microscope. The material was examined fresh, as it is otherwise very difficult to distinguish many of the more delicate organisms, although the need to work quickly has in many cases limited precision of identification. Somewhat similar quantitative examinations of the flora and fauna of small algal-covered areas or individual clumps of plants have been undertaken by Colman (1933, 1939) and Wieser (1952), but differences

in technique of collection and examination of material and in methods of expressing the results quantitatively make direct comparison with their findings very difficult. Even within the pool there are many factors to be taken into account in assessing any one sample - seasonal migrations and fluctuations of population, local movements caused by temporarily unfavourable conditions in that part of the pool, periodically atypical faunas due to high mortality in a preceding neap tide period, or an influx of animals from a lower tidal level during rough weather, as well as the amount of silt and detritus present. A quantitative sample is nevertheless much more satisfactory, if considerably more time-consuming, than subjective estimation.

(a) The Enteromorpha community of the fringe micro-zone

The fringe of Enteromorpha around the northern edge of the pool was examined in June 1952. This part is initially covered by the water of the pool, but usually left uncovered for several hours by the fall in level of the water during exposure. There was an undergrowth of very stunted Cladophora rupestris a few mm. high and a few small plants of Rhodochorton floridulum, the remainder of the sample being overwhelmingly Enteromorpha intestinalis plants to a length of about 8 cm., with a small admixture of other Enteromorpha species. Small nematodes, 1 mm. or less, were frequent, copepods and ostracods not uncommon, Rhombognathid

mites (probably almost exclusively Rhombognathides seahami) occasional, a few chironomid larvae, one or two turbellarians, several Fabricia sabella, a number of small gastropods (Omalogyrus atomus and Skeneopsis planorbis), a few of the small lamellibranch Turtonia minuta, ova of Skeneopsis, and egg-masses of Limapontia capitata, together with a few adults and a number of juveniles of the amphipod Hyale nilssoni. This is a relatively poor fauna: exposure to wave action and the small proportion of rhizoidal and filamentous algae inhibit the deposition of silt, as does the small number of Fabricia, an important silt-binding agent. Wave action, exposure to sun, rapid growth and unsubstantial texture of Enteromorpha, all contribute to inhibit epiphytes, and there is none apart from a few diatoms. The amphipod, Hyale nilssoni has a wide shore range, is very active both by night and day, and is commoner amongst fringing algae than in the pool itself. The mites are all herbivorous species and able to withstand a fair amount of desiccation, while the gastropods are small opisthobranchiates which customarily graze on green algae and are common or abundant in intertidal pools. The chironomid larvae are also herbivorous.

(b) The Open pool

Within the pool the silt deposit becomes thicker and the proportion of animal life increases: all the above-mentioned species, except for Hyale nilssoni, become more abundant, particularly the worm Fabricia and the small

nematodes which live-amongst silt and detritus, and small gastropods become especially numerous. The vegetation becomes denser with, in summer, tangled skeins of Rhizoclonium implexum and small pieces of plant and animal debris amongst it. Epiphytic diatoms become rather more common, particularly on the Rhodochorton.

(c) The Cladophora rupestris Community of the Shaded Parts

The most varied communities, however, are those formed by the perennial and pseudo-perennial plants of the shaded parts. The accompanying list (Text-fig.5) shows the results of a detailed examination in April 1953, of a 25 sq. cm. patch from a Cladophora rupestris community, with the approximate sizes of all plants and animals larger than 0.5 mm. As can be seen, the tufted, much branched growth gives protection for an extensive fauna, and the perennial lower parts provide a substratum for the attachment of many organisms, a feature more clearly shown amongst plants from deeper parts. The most striking features of the fauna living mainly amongst the algal fronds are the very large numbers of small gastropod molluscs and rhombognathid mites which feed on the Cladophora, and the numerous small lamellibranchs which find lodging on its branches. There are exceptionally few chironomid larvae - possibly a high proportion of the larval population had metamorphosed immediately prior to collection of the sample. Dinophilus

Species	No.	Size	Av.	Habitat
Monostroma grevillei	7	3-29 mm.	12 mm.	Epiphytic.
Enteromorpha compressa	14	5-40 mm.	18 mm.	On rock or epiphytic.
Rhizoclonium implexum	Considerable quantity			Amongst Cladophora fronds.
Cladophora rupestris	30	6-36 mm.	15 mm.	Epiphytic.
Filamentous diatoms	Present, not abundant.			Epiphytic.
Ceramium rubrum	1	15 mm.	15 mm.	Epiphytic.
Gromia oviformis	11	1.5-2.0mm.	1.7 mm.	On rock or basal fronds.
Unidentified foraminifera	1	1 mm.	1 mm.	Not known.
Coryne muscoides (colonies)	3	3-15 mm.	8 mm.	Attached to basal parts of Cladophora.
Macrostomum hystrix	3	1-3.5mm.	2.5mm.	Amongst silt.
Plagiostomum vittatum juvenile.	25	-	-	Amongst silt.
Echinoderis dujardini	22	-	-	Amongst silt.
Nematoda	820	-9mm.	1.5mm.	Amongst silt.
Bowerbankia imbricata	28			Attached to basal parts of Cladophora.
Littorina spp.,young	2	-1mm.	0.7mm.	Amongst algal fronds.
Skeneopsis planorbis & Omalogyra atomus	213	0.5-2.0mm.	1.3mm.	Amongst algal fronds.
S.planorbis ova	88	-	-	Attached to Cladophora.
Limapontia capitata	69	0.5-2.5mm.	1 mm.	Amongst Cladophora fronds.
L.capitata spawn masses	3			Attached to Cladophora near base.
Mytilus edulis, young & Turtonia minuta	549	-4 mm.	0.7mm.	Attached in axils of Cladophora branches.
Dinophilus taeniatus	22	-1 mm.	0.7mm.	Amongst silt and fronds.
Harmothoë imbricata	1	1 mm.	1 mm.	Amongst silt.
Indet. post-larval polychaetes	2	-1 mm.		Amongst silt.
Fabricia sabella	79	-3.5 mm.	2 mm.	Amongst silt and basal fronds.
Spirorbis borealis	4	-2mm.	1 mm.	Attached to Cladophora.
Ostracoda	155	-1mm.		Amongst silt and fronds.
Copepoda	192	-1mm.	0.8mm.	Amongst silt and fronds.
Idotea sp.	2	3mm.	3mm.	Amongst algal fronds.
Stenothoë monoculoides	13	2.0-2.5mm.	2.2mm.	Amongst algal fronds.
Hyale nilssoni	1	7mm.	7mm.	Amongst algal fronds.
Clunio marinus larvae	4	2.5-4.5mm.	3.5mm.	Amongst algal fronds.
Indet. larval arthropod.	6	-	-	Amongst silt.
Rhombognathid mites	334	-	-	Amongst algal fronds.
Halacarus basteri	4	1 mm.	1 mm.	Amongst silt and rhizoids.
Copidognathus fabriciusi	7	0.5 mm.	0.5mm.	Amongst silt and rhizoids.
Indet. ova	1	1 mm.	1 mm.	Not known.

Tex-fig.5. Flora and fauna of Cladophora rupestris community, 0930 hrs., 18.4.52. Area = 25 sq.cm. Depth = 7 cm. Wt.of cleaned, damp algae 2.25 gm.

taeniatus is also poorly represented: the winter population is very much greater. Hyale nilssoni is seen to be replaced by the small active scavenger Stenothoë monoculoides, which is still more numerous in the deeper communities, in which it is normally accompanied by juvenile stages of the larger Apherusa jurinei.

(d) The Polysiphonia nigrescens Community of the Deeper Parts

The great disturbance to the pool, the long-lasting effects on the particular area cleared, and the very varied and dense populations in the communities of the deeper parts, made similar experimental clearings impracticable for these areas. However, the accompanying table (Tex-fig.6) shows the associated algae and fauna of a small undetermined area cleared in the Polysiphonia nigrescens community of one of the deepest parts of the pool, in March 1952. It is difficult to count individual plants, and the number here given refers to erect shoots from the network of basal rhizoids. It is, of course, a very much smaller sample than that from the Cladophora community, and since it was collected a month earlier in the year, direct comparison is rather difficult. The number of small lamellibranch molluscs is proportionately much higher, but of gastropods is rather less. Limapontia capitata is completely absent, as could be expected both from feeding habits and seasonal occurrence. Dinophilus taeniatus is much more abundant, but this is certainly a

Species	No.	Size	Av.	Habitat
Monostroma grevillei	Freq.	Small		Epiphytic.
Cladophora rupestris	Few	To 15mm.		On rock.
Synedra sp.	Occ.			Epiphytic.
Grammatophora sp.	Rare			Epiphytic in short chains.
Naviculoid diatoms	Few			Amongst silt.
Ectocarpoid sp.	Few			Epiphytic.
Rhodochorton floridulum	Few			Basal, entwined
Ceramium rubrum	6	Minute		Epiphytic.
Polysiphonia nigrescens	24	30-60mm.	45mm.	On rock
Laurencia hybrida	Few	To 5mm.		Epiphytic.
Dynamena pumila	1	8mm	8mm	Basal, on Polysiphonia.
Turbellaria	5	0.5-1.0mm.	0.7mm.	Amongst rhizoids
Nematoda	103	-2.5mm.	1mm.	Amongst silt and rhizoids.
Rissoid sp.	1	2mm.	2mm.	Amongst fronds
Littorinid sp.	4	1.0-1.5mm.	1.3mm.	Amongst fronds
Skeneopsis planorbis & Omalogyra atomus	16	0.5-1.5mm.	1.0mm.	Amongst fronds
Mytilus edulis young & Turtonia minuta	147	-3.0mm.	1.0mm.	Attached to fronds
Dinophilus taeniatus	33	-1.0mm.	0.6mm.	Amongst silt & fronds.
Fabricia sabella	7	1.0-3.0mm.	1.5mm.	In tubes amongst rhizoids
Spirorbis borealis	21	0.5-2.0mm.	1.0mm.	Attached to fronds
Ostracoda	33	-1.0mm.		Amongst silt and fronds
Copepoda	13	-1.5mm.		Amongst silt and fronds
Larval copepoda	2			Amongst fronds
Idotea sp.	20	2.0-4.5mm.	3.5mm.	Amongst fronds
Stenothoë monoculoides	3	1.5-2.0mm.	1.7mm.	Amongst fronds
Clunio marinus larvae	2	4.0-5.0mm.	4.5mm.	Amongst fronds
Rhombognathid mites	39			Amongst fronds

Text-fig.6. Flora and fauna of Polysiphonia nigrescens clump, 21.3.52.
Depth 20cm. Wt. of cleaned, dried algae 0.22 gm.

seasonal effect. The most striking difference is in the presence of a large number of juvenile Idotea: in the pool these are almost always restricted to Polysiphonia nigrescens and the Ceramium rubrum epiphytic on it. Their colouring normally matches that of the Polysiphonia, and the thickness and growth form of the fronds seem peculiarly suited to their size and mode of progression. The increased number of Spirorbis borealis is due to the main axes of the Polysiphonia being relatively more rigid than those of the Cladophora.

(e) Communities of the Ledge Micro-facies

The densely matted, low-growing communities of the ledges are yet more difficult to examine quantitatively, owing to the irregular, mainly coralline substratum. The population is still more varied, especially amongst Codium and Sphacelaria pennata var. fusca, both of which form thickly matted tufts. Amphipods and mites are less numerous, the latter including a much higher proportion of carnivorous forms, but small and juvenile annelids of many species occur here, together with several species rarely encountered elsewhere in the pool, such as the small brittle-star Amphipholis squamata and the pycnogonids, mainly Anoplodactylus pygmaeus.

(f) Communities of Molluscan Shells

One other rather specialised communal relationship between plants and animals of the pool remains to be mentioned - that of the algae growing on and within the periostracum of molluscs. The few small limpets present in the pool do not appear to form 'islands of vegetation' as described by Knight and Parke (1931), and as specimens in pools elsewhere on the shore frequently do. The periostracum of the littorinids often carries numerous minute sporelings of Fucus, Entermorpha and other species, which do not normally develop very far, while a few species, (Gomontia polyrhiza, Tellamia contorta, Ostreobium quekettii, and Entophysalis crustacea), have only been recorded within the pool in the periostracum of one or two of the larger molluscs, though they may also be expected to occur upon the few small barnacles of the pool (Parke and Moore, 1935).

2. Neap Tide Exposures

As already abundantly indicated, the period of neap tides is a highly critical one, particularly during spring and early summer. During the spring there is a rapid growth of annual and ephemeral and regeneration of pseudo-perennial plants, with more or less severe set-backs, particularly to the vegetation of the shallow northern side, during prolonged exposure of the pool, depending on the length

of exposure and prevailing weather conditions. Eventually, however, at some time between late March and early May, poor neap tides coincide with calm seas and bright sunshine: the water level falls very low, or the pool dries out completely, and the algae of the deeper parts are suddenly faced with high temperatures and the risk of desiccation. For instance, when the pool dried out completely on March 25th, 1953, (Figs.4, 7, 23) the Polysiphonia nigrescens plants of the largest community were exposed to a temperature which reached 17.5°C on the surface and 14.75°C underneath the fronds, at a time when the surface sea temperature was only about 7°C. Such extreme conditions produce dramatic and profound changes in both flora and fauna. During exposure many annelids and amphipods can be found dead or in a moribund condition in the pool, and doubtless small shore birds account for many more, as already postulated. The first plants to show visible ill effects are generally Ceramium rubrum, followed by Ulva lactuca and the fringing Enteromorpha. Nearly all plants in and around the pool eventually show signs of damage under such conditions: the ephemeral and annual plants may be almost eliminated, and the perennial and pseudo-perennial plants may be killed or so severely affected that recovery is very much slower than usual, so that the entire seasonal rhythm of the growth of pool vegetation may depend ultimately on events over a few days in spring. Thus in 1950-52 Polysiphonia nigrescens

maintained a flourishing community which died back to the older parts in March or April, virtually disappeared during the summer and autumn under a heavy covering of epiphytes (Fig.46), and produced fresh fronds during the winter. Under favourable conditions the plants were able to reproduce before being again killed back to their older parts. But in 1953 the complete drying out of the pool caused the death of the entire plants, and they were later replaced by a mixed population of other species, as shown in Figs.14 and 15. From the second chart it can be seen that the once dense community had barely begun to reform by the spring of 1954, the plants represented being young and small. This in turn affected the fauna of the pool, since several species, e.g. Amphithoë rubricata and Idotea sp., were rarely found elsewhere. The Cladophora rupestris communities were not completely destroyed, but suffered a severe and prolonged set-back, while the annual Dumontia incrassata, which is usually abundant throughout April and even present in June, was totally eliminated. The effect on reproduction was also considerable, since many specimens were killed before they could form or liberate their spores or other reproductive bodies.

Amongst the fauna the population is profoundly affected by such conditions. It is rapidly restored for errant species such as Leander squilla and Stenothoë monoculoides, though for others, e.g. Limapontia capitata

and Apherusa jurinei, replenishment is slow, or does not take place till the autumn, as for Dinophilus taeniatus. Molluscs and halacarids seem little affected, but annelids and amphipods (except for Hyale nilssoni) suffer severe reduction in numbers.

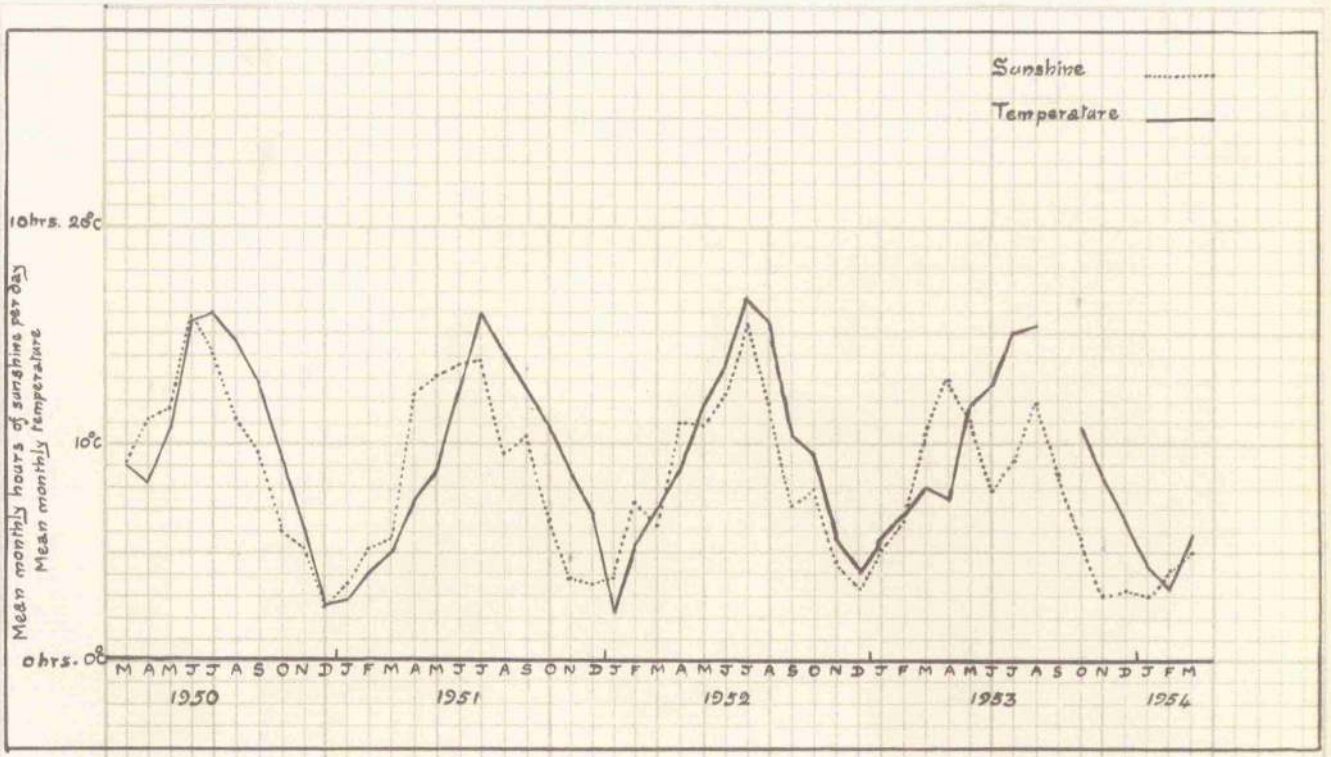
3. Population Changes from Year to Year

Seasonal changes in population have already been referred to in several sections, especially with regard to the vegetation in general and the communities in particular. Variations in the seasonal cycle from one year to another have not been discussed, however, apart from a few very specific instances.

That there is an annual pattern of vegetation in the pool, with recognisable seasonal aspects reappearing each year, has already been indicated. Changes may appear, however, either in the nature of the vegetation or in the time at which a particular growth stage is reached. Small local variations may be brought about in many ways, notably by erosion of the substratum, and are of relatively less interest than alterations in the seasonal rhythm, the growth or disappearance of certain species being either delayed or precocious owing to unusual seasonal conditions, such as a particularly mild winter or dull summer. These changes are particular instances of a general condition of the

vegetation of the entire shore at such times. The accompanying figure (text-fig.7), constructed from data kindly supplied by the Burgh Surveyor, St.Andrews, shows monthly mean temperatures and hours of sunshine per day for St.Andrews during the period concerned. This shows that temperature changes are in general more uniform than light conditions, due to the stabilising influence of the sea. There are several features of special interest. The high insolation with relatively low temperatures in April and May of 1951 encouraged a particularly fine growth of the spring algae, although this was offset by very unfavourable neap tide conditions in mid-April. It is noteworthy that the two recorded instances of reproduction of Polysiphonia nigrescens occurred under such conditions, in April 1951, and in March 1953. The most outstanding features of 1952 were the very dull September and cold November. Possibly the former inhibited reproduction, and hence delayed the death, of the summer annual Asperococcus fistulosus, for the long survival of small plants of this species, still present as late as December, was particularly marked. The relative luxuriance of Polysiphonia nigrescens plants during this winter and the appearance of small thalli amongst the Codium growths as early as September may have been due to the low autumn temperatures permitting regeneration to proceed earlier and more rapidly than usual.

The year 1953 was exceptional in many ways. The very



Text-fig.7. Graph of monthly mean temperatures and hours of sunshine per day, March 1950 - March 1954.

sunny and warm weather of March and April encouraged precocious metamorphosis of chironomid larvae, but led to the early and severe destruction of the spring vegetation referred to in the preceding section, while the dull, rather cool summer probably favoured the development of the algae and sedentary animals of lower levels which succeeded in developing in the pool at this time, such as Laminaria digitata (July, August) and Rhodomela confervoides (October, November) and the ascidians Ascidia conchilega (September) and Sidnyum turbinatum (July). The unusually mild, dull winter was probably responsible for the complete failure of Codium to develop thalli, the presence of young Asperococcus fistulosus plants in February 1954, and of occasional specimens of the nudibranch Limapontia capitata throughout the winter, and, just possibly, the very retarded development of erect filaments from the creeping rhizoids of Polysiphonia urceolata, though the latter might more probably have been due to the widespread damage and destruction caused by conditions in the earlier part of the year. The mild winter followed by very cold weather in February may have been responsible for the general lateness in development of the spring vegetation. Thus Monostroma grevillei did not appear until March, though usually frequent in February, Ceramium rubrum, though present and quite well grown, was sterile throughout February, and the thick spring growth of Enteromorpha compressa admixed with E. intestinalis

normally characteristic of the pool in March did not begin to appear until April.

4. A Comparison with the Flora and Fauna of Neighbouring Habitats

Although the majority of the nearby pools are of a broadly similar structure, differences in size, depth, drainage, tide level and in many other factors create very diverse environments. A detailed comparison of these with the pool under discussion would be outside the scope of the present work, but the distribution of many species of both plant and animal presents interesting problems.

Many of the algal species abundant in neighbouring pools and on nearby rocks at almost the same level are very poorly developed, rare or completely absent from the pool flora. For the Rhodophyceae which extend their vertical range on the shore by growing in pools in the shade of over: :hanging banks and large algae, it is probable that even in the deepest parts temperature changes are as a rule too extreme for survival over the late spring and summer, and that the zone under the southern bank in which light conditions are generally suitable is too narrow and variable for settle: :ment by such species to be other than casual and fortuitous. Species in this category which have not so far been found at all in the pool are Phycodrys rubens (Huds.) Batt., Plocamium coccineum (Huds.) Lyngb. and Griffithsia flosculosa (Ellis) Batt., while Membranoptera alata and Phyllophora membranifolia have occurred only rarely, as very stunted individuals with a short life span. Polyides caprinus can barely survive as small, sterile individuals, though growing

well and reproducing freely in a smaller but deeper neighbour:
:ing pool. The larger brown algae of pools either cannot develop here at all (e.g. Halidrys siliquosa (L.) Lyngb.), are rare and short-lived (Laminaria digitata) or occasional and stunted (Fucus serratus), and again, temperature fluctuations appear the most probable deterrent, as postulated by Lami (1941). The most difficult case to interpret is the absence or very poor growth of Pylaiella littoralis, which is abundant on rocks at lower levels and in pools both higher and lower on the shore, epiphytic on various algae. It seems just possible that the turbulent water conditions while the pool is covered are too strong for settlement on some hosts, and competition from other epiphytes too keen on others, but neither hypothesis is very convincing.

Many of the algal species occurring in the pool are represented by plants at all times markedly smaller than normal specimens from other habitats, and sometimes have correspondingly smaller cells, particularly in the case of filamentous algae such as Chaetomorpha melagonium and Rhodochorton floridulum, in one specimen of the former being as little as one third of the minimum size given by Newton (1931); this emphasises the danger of using cell measurement as the main criterion for identification of species. The shallowness of the pool, the frequent turbulence of the waters which cover it and the friability of the substratum militate against the development of large plants, particularly

in isolation, and the growth season is often cut short by adverse conditions, which do not affect the neighbouring pools, all at lower levels. so drastically.

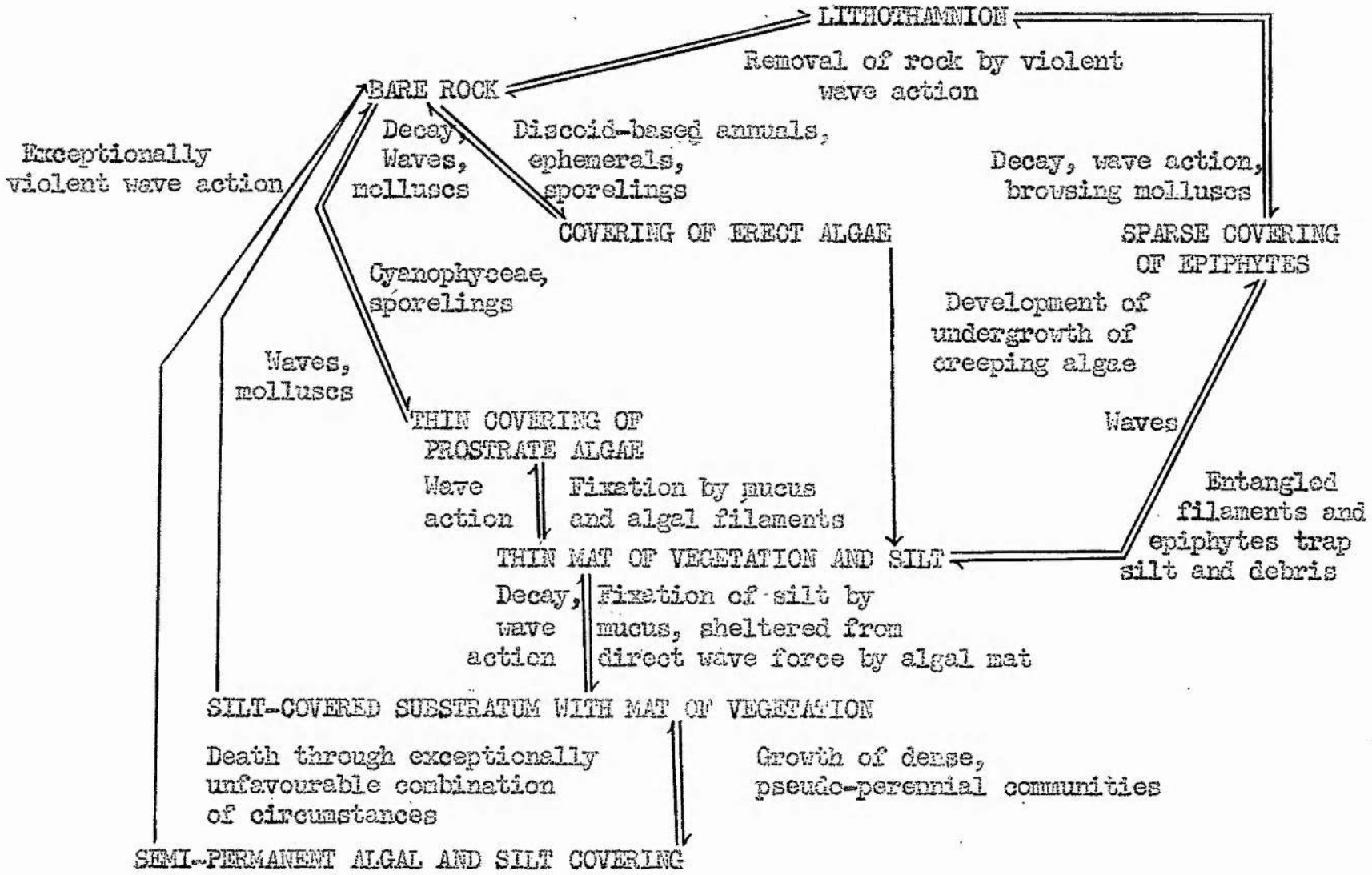
The faunas of these other pools have not been studied closely. As might be expected the larger, deeper pools with a preponderance of Phaeophyceae and Rhodophyceae harbour larger and more numerous specimens of many species which are rare or occur only as juveniles in this particular pool (e.g. Kefersteinia cirrata, Apherus jurinei, Amphithoe rubricata, Amphipholis squamata), as well as many which have not been found in it at all (e.g. Apherusa cirrus Bate, which is most frequently associated with Halidrys siliquosa). On the other hand the smaller proportion of Chlorophyceae is probably responsible for a corresponding decrease in the numbers of certain species (e.g. Chironomid larvae, Limapontia capitata, Rhombognathid mites).

CONCLUSIONS

The biotic relationships of the flora and fauna of the pool and their environment are necessarily dynamic. This intensive study over the period June 1950 to March 1954 has shown that three major trends of distributional change may be distinguished, controlled primarily by substratum, tides and seasonal factors respectively.

The first is summarised by the diagram of text-fig.8, showing the very complex cycle of colonisation from bare rock to the semi-permanent covering of dense algal communities, in which the accumulation of a protective layer of silt, mucus and algal rhizoids and filaments is offset by the destructive action of browsing molluscs and, above all, by wave force. The part which animals play in this cycle is, however, of considerable importance. Their depredations are probably rarely lethal to large, healthy plants, but must account for vast numbers of spores, sporelings and unicellular plants (Fig.49). The silt-binding properties of the mucous secretions of various annelids and nemertines have already been stressed: on the other hand the burrows of the larger animals, particularly Venerupis saxatilis, may seriously weaken the rock and assist the destructive forces of the waves.

Tidal rhythm controls the extent to which other factors may exercise their influence on the pool: the critical period



Text-Fig. 8. Diagram to illustrate vegetative colonisation and succession from bare rock.

is during the prolonged exposures of neap tides, the porous nature of the soft sandstone making the pool particularly vulnerable to desiccation at such times. The role of neap tides is therefore as a possibly lethal factor interfering with and influencing the normal seasonal changes in the flora and fauna, particularly in spring and early summer. Not only may growth be arrested and plants destroyed, but sexual and asexual reproduction may often be prevented, while sporelings are probably more vulnerable than adult tissues to adverse conditions. This may explain the prevalence of vegetative reproduction amongst the principal community-forming plants of the pool. The importance of the height of extreme (low) high water neap tides as a critical level for life between the tides, as reported for Wembury by Colman (1935) and for Aberystwyth by David (1941), is therefore supported by these observations.

Seasonal changes provide the general pattern within which the other trends operate. The poor conditions for photosynthesis in winter, coupled with damage to tissues by silt, heavy seas and the resident fauna, restrict the winter growth, which is dominated by Rhodophyceae and the pseudo-perennial Chlorophyceae. As light increases while temperatures remain low, an increasingly favourable balance of photosynthesis over respiration becomes possible, leading to an outburst of regenerative growth amongst the pseudo-perennial plants in the late winter and spring. This is

latterly accompanied by an influx of spring annuals and a great increase in size and abundance of the Chlorophycean ephemerals, the pool becoming more and more dominated by Chlorophyceae. The growth of the Rhodophyceae and other winter and spring plants is generally terminated more or less catastrophically by unfavourable neap tide conditions occurring at some time between late March and mid-April, and thenceforward the dominant vegetation consists of ephemerals and summer annuals, the perennating basal parts of the community-forming plants being generally covered with transient epiphytic growths which doubtless help to shield them from extremely unfavourable conditions. The higher angle of incidence of direct sunlight progressively decreases the amount of shade, and the Chlorophycean ephemerals encroach correspondingly further on this area, while high temperatures and insolation cause the shallow, illuminated northern side to become increasingly more barren. During the autumn there is a fresh outburst of growth of the ephemeral Chlorophyceae, probably associated with the decreased risk of desiccation, and some of the pseudo-perennials plants begin to show new growth. The ephemeral Chlorophyceae become progressively smaller (figs.28-30) and less abundant, until the winter aspect is once more assumed.

One final point may be stressed. The pool has been shown to provide a considerable range of environmental conditions both within the pool at any one time, and at

different times, states of the tide, seasons and years. The nature and condition of the algal and faunal population fluctuate correspondingly, and to arrive at any understanding of the composition of the flora and fauna at any one time it has been necessary to consider not only the contemporary environment but also circumstances which have affected the pool over a considerable preceding period. General conclusions drawn from short-term studies of populations should therefore be treated with some caution, since they may in part be based on temporary and unusual conditions: several years of observation are required before the general seasonal cycle of vegetation and animal life in such a habitat can be distinguished with any confidence within the complex and intricate pattern of the inter-relationships of organisms and their environment.

SUMMARY

Literature dealing with rock pools is scanty, and as a rule they have been studied either very generally or over a rather short period of time. During the course of the present work a single pool, 3.7 x 1.5 m., just below high water neap tide level on the St.Andrews shore, has been studied in detail from June 1950 to March 1954, in an endeavour to correlate changes in flora and fauna with variations in environmental conditions. The location and topography, periods of exposure, illumination, temperature, hydrogen ion concentration and salinity have been measured to a greater or lesser extent, and observations made or estimations formed of the probable importance of desiccation, wave action, dissolved oxygen concentration, inorganic substances other than chlorides in solution, organic matter present, and biotic factors. It has been shown that conditions vary very considerably from one part of the pool to another at any one time, and in particular parts at different times of the day or seasons of the year, and that various factors are so closely linked in their effects that they cannot usefully be considered independently.

An ecological classification of the pool vegetation has been evolved which emphasises the parallel between the range of conditions (and hence of types of algal growth) within the pool and on the shore in general. The high

incidence of epiphytism is considered in some detail, and its importance and effects in the case of both host and epiphyte assessed. Healthy plants seem less liable to epiphytic settlement than unhealthy specimens: species which are generally epiphytic do not as a rule thrive in other situations, and vice versa: the principal danger to the actual life of the host plant seems to lie in the greater liability to removal, due to increased resistance to wave force. Comparison of the life cycles within the pool of the various algal species has shown the prevalence of vegetative reproduction, including regeneration, from perennial basal parts, amongst the community-forming plants of the pool.

The flora (80 species identified, including 24 unpublished St.Andrews records) and the fauna (98 identified, including 35 unpublished) are listed, with notes on times of occurrence, frequency, habit, size, reproduction and other noteworthy features, and additional notes are provided amplifying these details for species of particular nomenclatural, taxonomic or ecological interest.

The relations between plants and animals are considered in further detail, with reference to quantitative samples of the flora and fauna taken from time to time. Faunal populations are shown to vary amongst different types of vegetation, and in some cases to be closely dependent on the presence of particular algal species.

The vital importance of atmospheric conditions during the prolonged exposure of the pool at times of poor neap tides is illustrated and discussed. High water neap tide level is considered to be highly critical for the flora and fauna of rock pools. The seasonal cycle of vegetation and the faunal population of the pool are shown to have varied somewhat from year to year, and an attempt is made to correlate these changes with the correspondingly exceptional meteorological conditions.

Species frequent in neighbouring pools but rare or absent in the case of this particular pool are instanced and discussed. Temperature fluctuations are considered to be probably the most important limiting factor for the majority of the algae concerned. The generally stunted nature of the vegetation and frequently reduced cell size are attributed primarily to the shallowness of the pool, exposure to violent wave action, and adverse conditions during the normal growing season. Browsing animals constitute a serious menace to spores, sporelings and minute plants, but are probably rarely lethal where the larger plants are concerned.

The dynamic nature of the relationships of the population to its environment is stressed. Three main trends of change are shown to exist in the pool: the complex succession from bare rock to semi-permanent covering by a dense algal community, the catastrophic effects of neap tide conditions, especially during spring and early summer, and the more or less regular

seasonal succession of vegetative changes. Particular stress is placed on the importance of long-term observations in assessing the distribution of population within this type of habitat.

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PLATE I. GENERAL TOPOGRAPHY

Fig.1. The Hind Rock, showing general rock formation.

2. Top of Hind Rock from landward end, showing series of pools, March 1953.

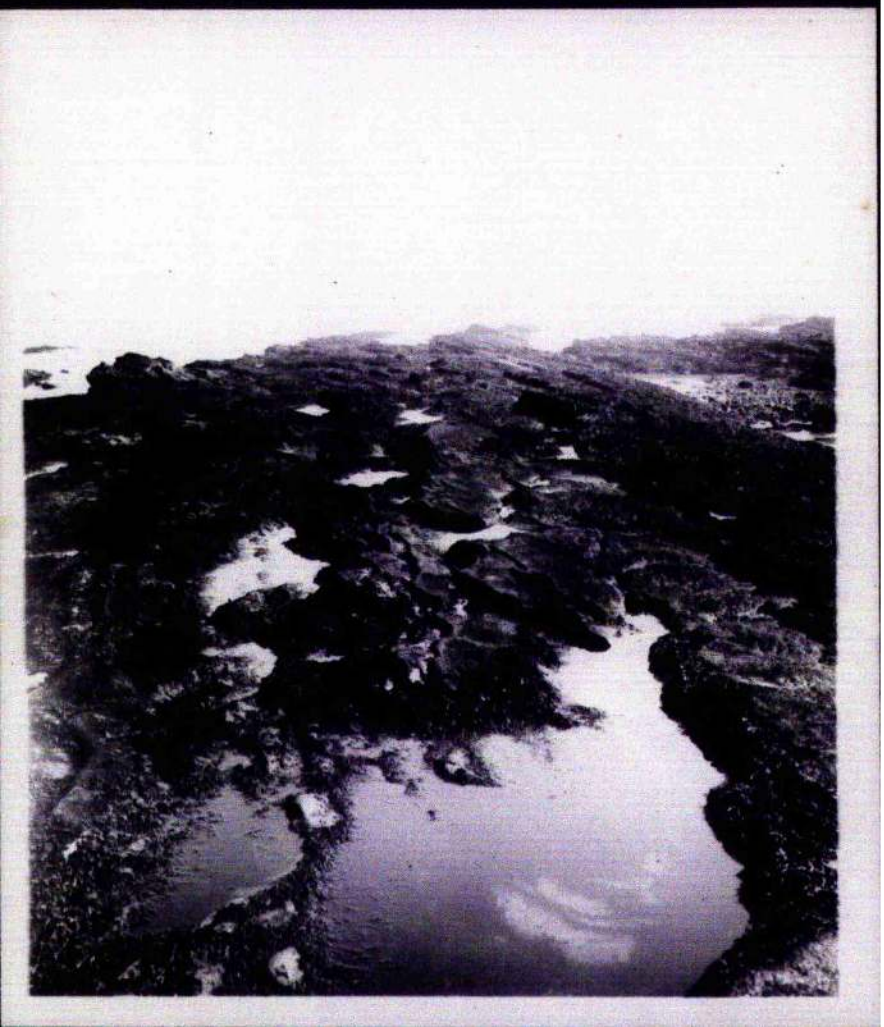


PLATE II. TOPOGRAPHY OF THE POOL

Fig.3. Pool from landward end, showing position relative to steep northern face of Hind Rock, 22nd May 1953.

4. Pool from seaward end, dried out during a period of very poor neap tides, 25th March 1953.

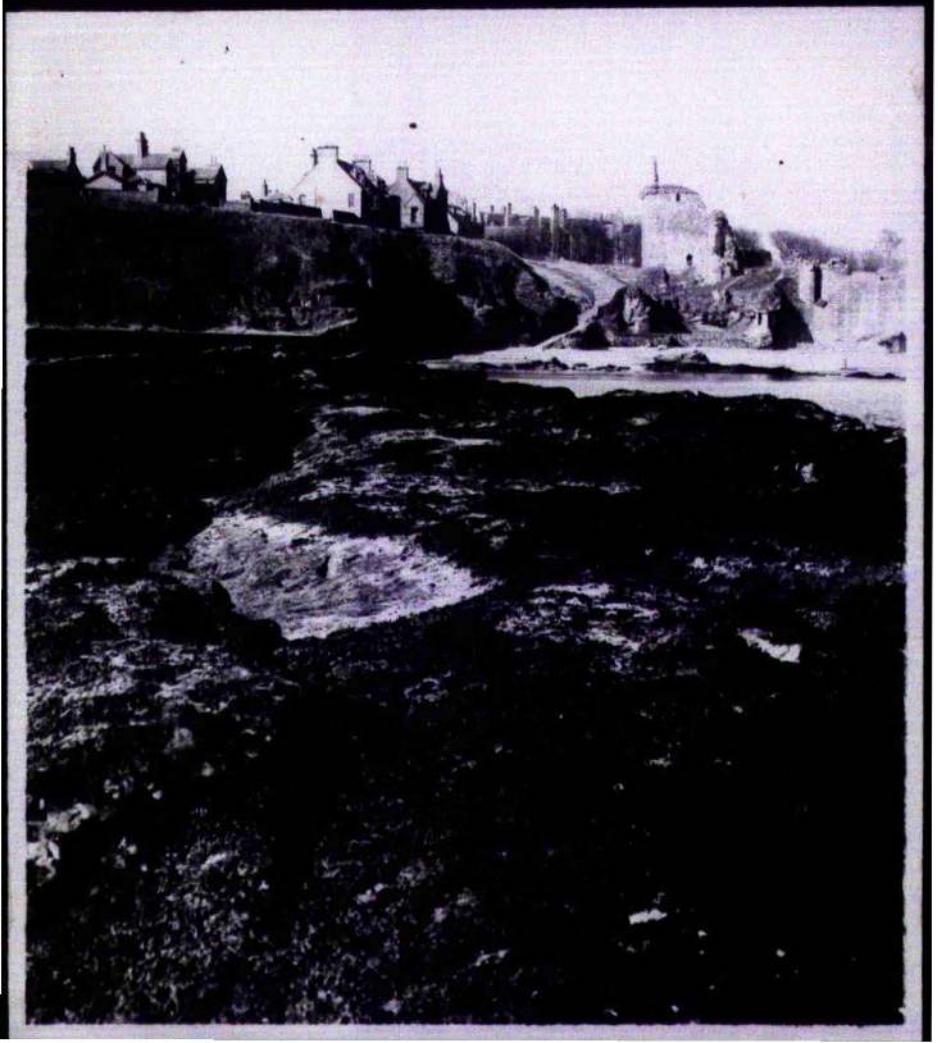


PLATE III. TOPOGRAPHY OF THE POOL

Fig. 5. Pool, with normal water level, 10.45 hrs., 20th March 1952.

6. Pool, with considerably lower level, 11.30 hrs., 9th March 1953.

7. Pool, seaward part, showing central ledge, completely dried out, 10.45 hrs., 25th March 1953.

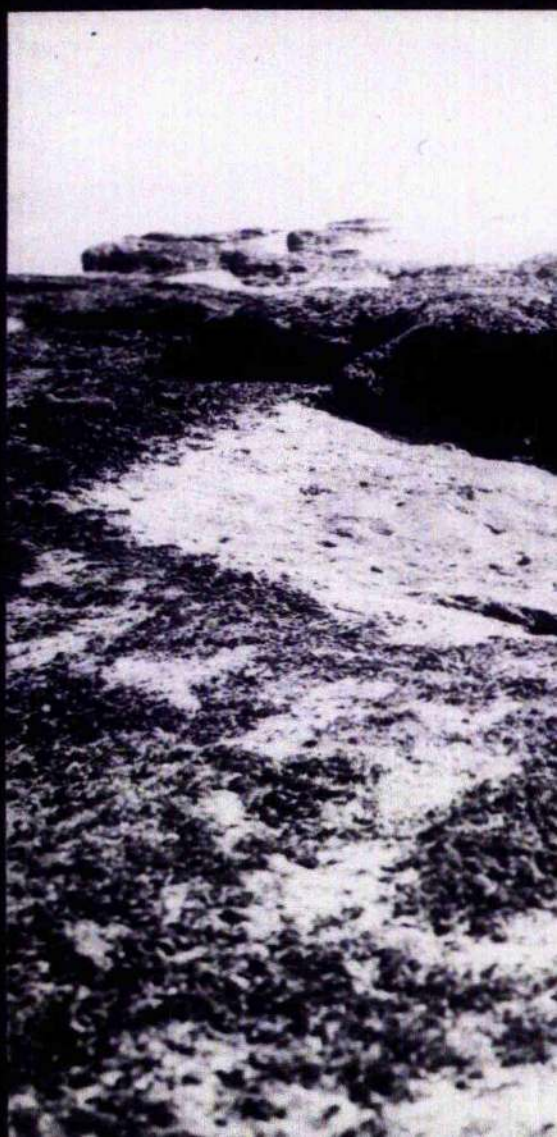


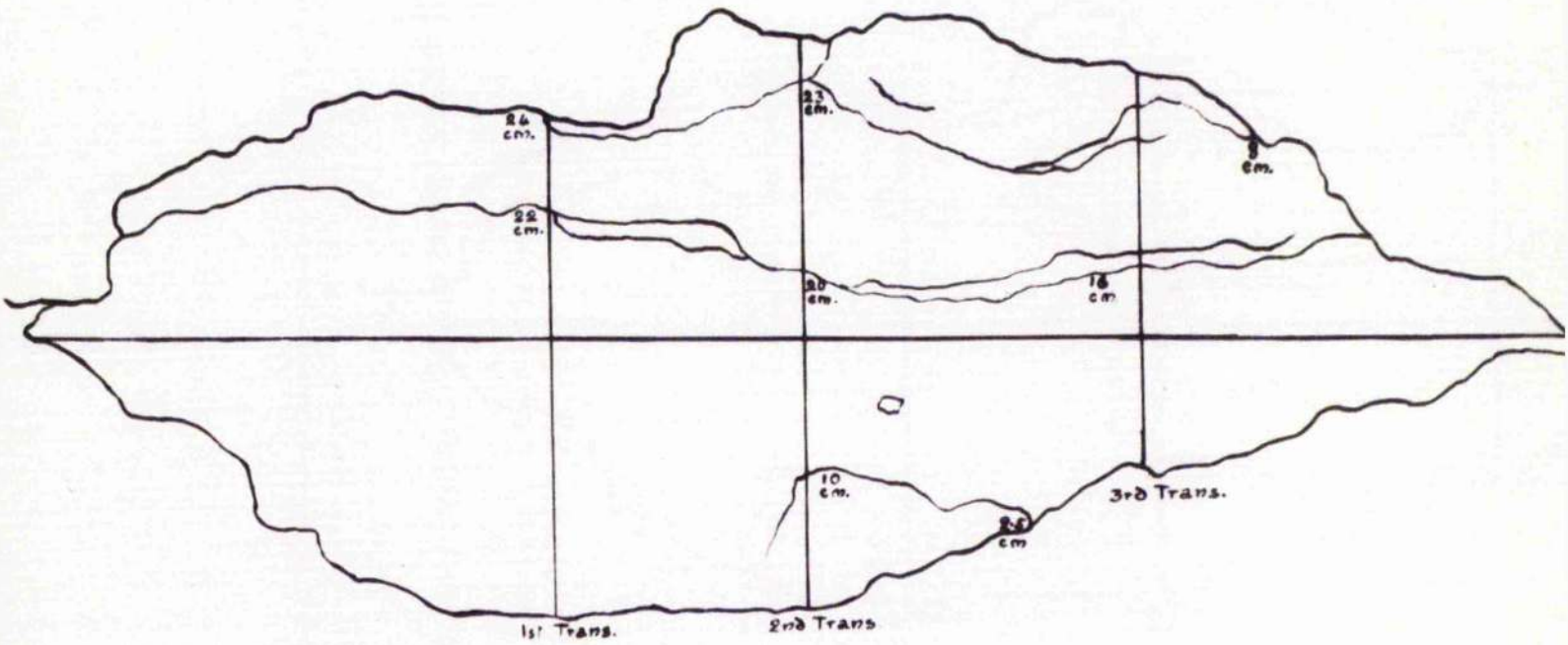
PLATE IV. TOPOGRAPHY OF THE POOL

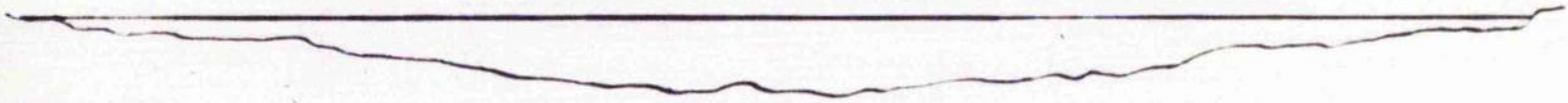
Fig.8. Contour charts of pool:

(a) Area chart, showing positions of transects and depth at various points shortly after exposure of pool.

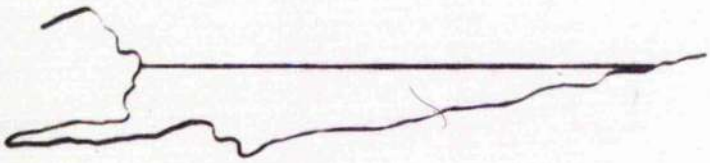
(b) Longitudinal transect of pool.

(c), (d), (e) Transverse transects.

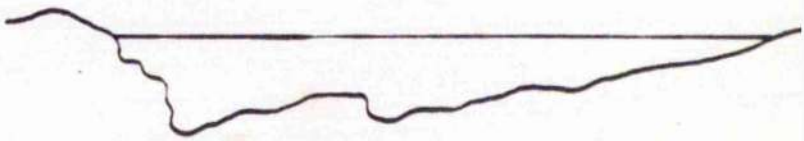




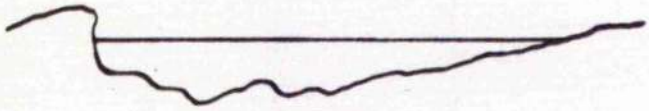
Longitudinal Transect



1st Transect



2nd Transect



3rd Transect

Scale : 1 metre

PLATE V. WAVE ACTION

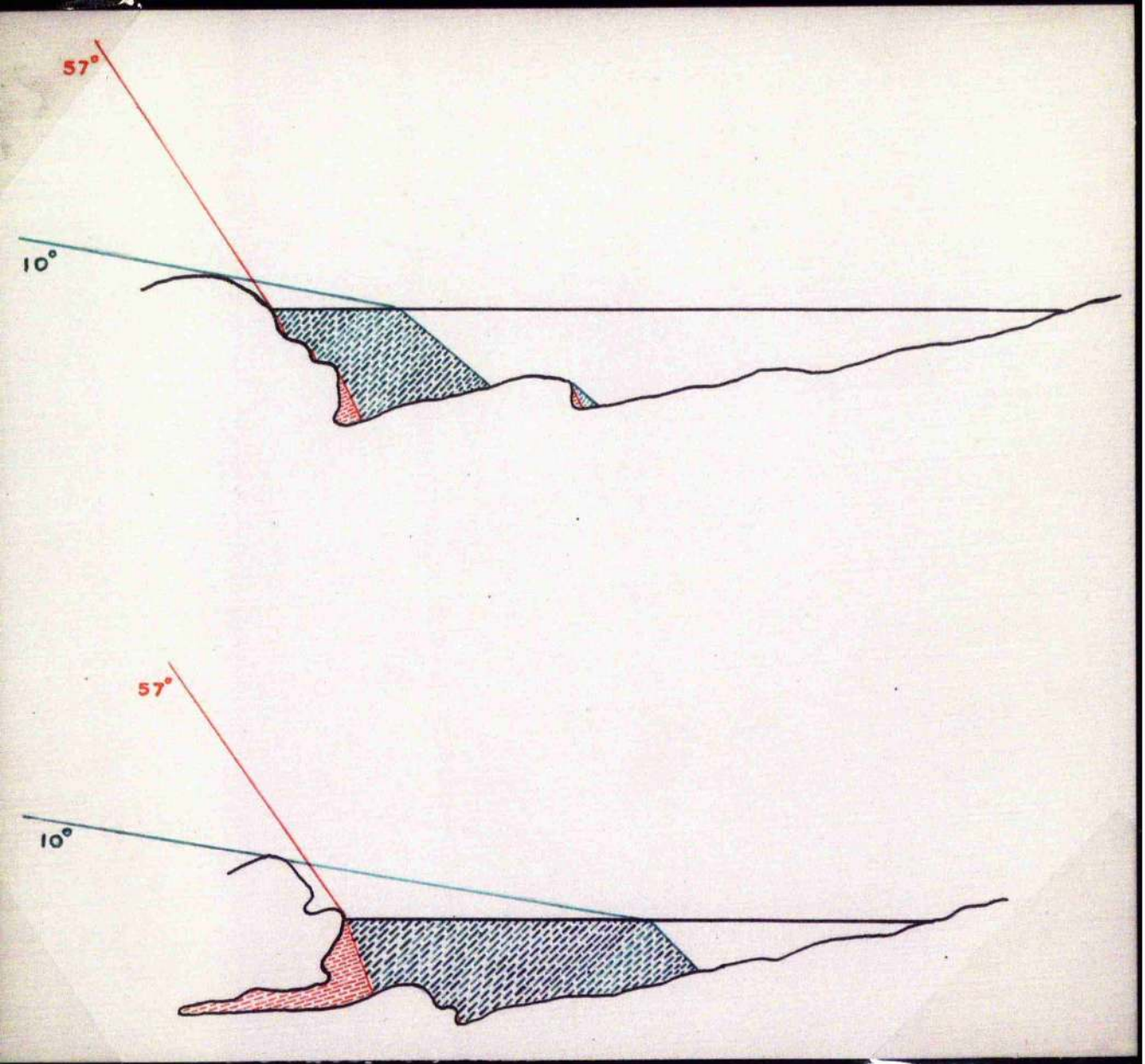
Fig.9. Waves breaking over the pool.

10. Diagram to show directions in which waves normally break over pool, as in Fig.9.

PLATE VI. LIGHT

Fig. 11. Circuit diagram of apparatus for measuring intensity of illumination within the pool.

Fig. 12. Diagram to show the angle of incidence of direct sunlight at midday in midwinter (green) and midsummer (red).


57°
10°

57°
10°

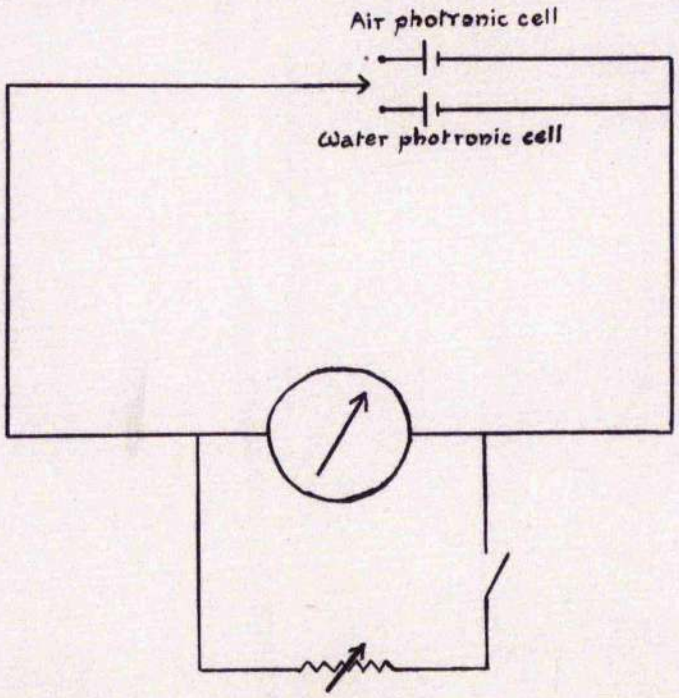
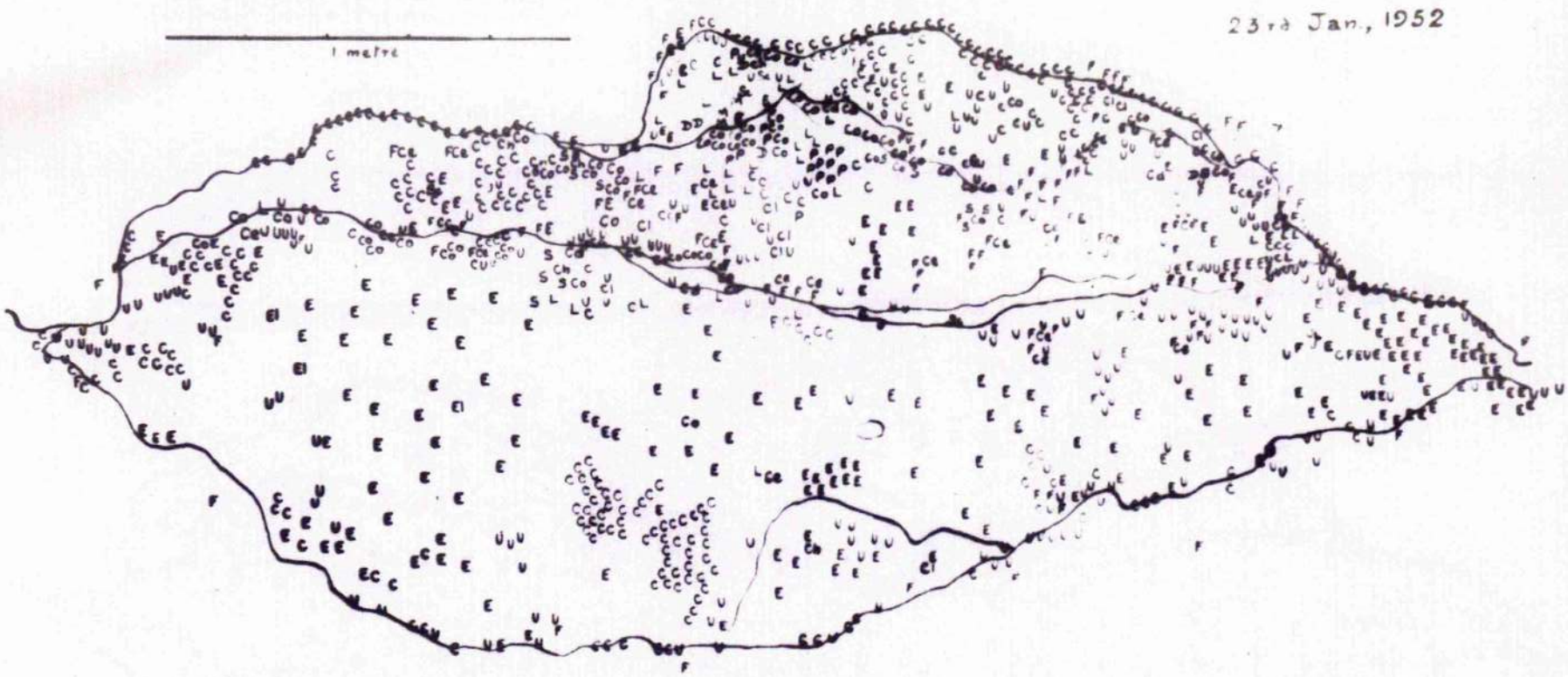

Air photronic cell
Water photronic cell

PLATE VII. FLORA OF THE POOL

Fig. 13. Chart to illustrate density and distribution of macroscopic algae within the pool in January 1952. (In order to simplify the chart the ground vegetation of Rhodochorton floridulum and Lithothamnion lenormandii has been omitted).



B = Bryopsis plumosa
C = Cladophora rupestris
Cd = Codium tomentosum
Ce = Ceramium rubrum
Ch = Chondrus crispus
Cl = Cladosteubus spongiosus
Co = Corallina officinalis
D = Dumontia incrassata
E = Enteromorpha spp
El = Enteromorpha linza
F = Fucus spp
L = Laurencia hybrida
M = Monostroma grevillei
P = Polysiphonia nigrescens
Pu = Polysiphonia urceolata
S = Sphacelaria pennata var fusca
Sc = Scytosiphon lomentaria
U = Ulva lactuca

PLATE VIII. ALGAL COMMUNITIES

Fig. 14. Chart to show the configuration of the pool and size of the principal communities of perennial and pseudo-perennial plants within it in March 1952.

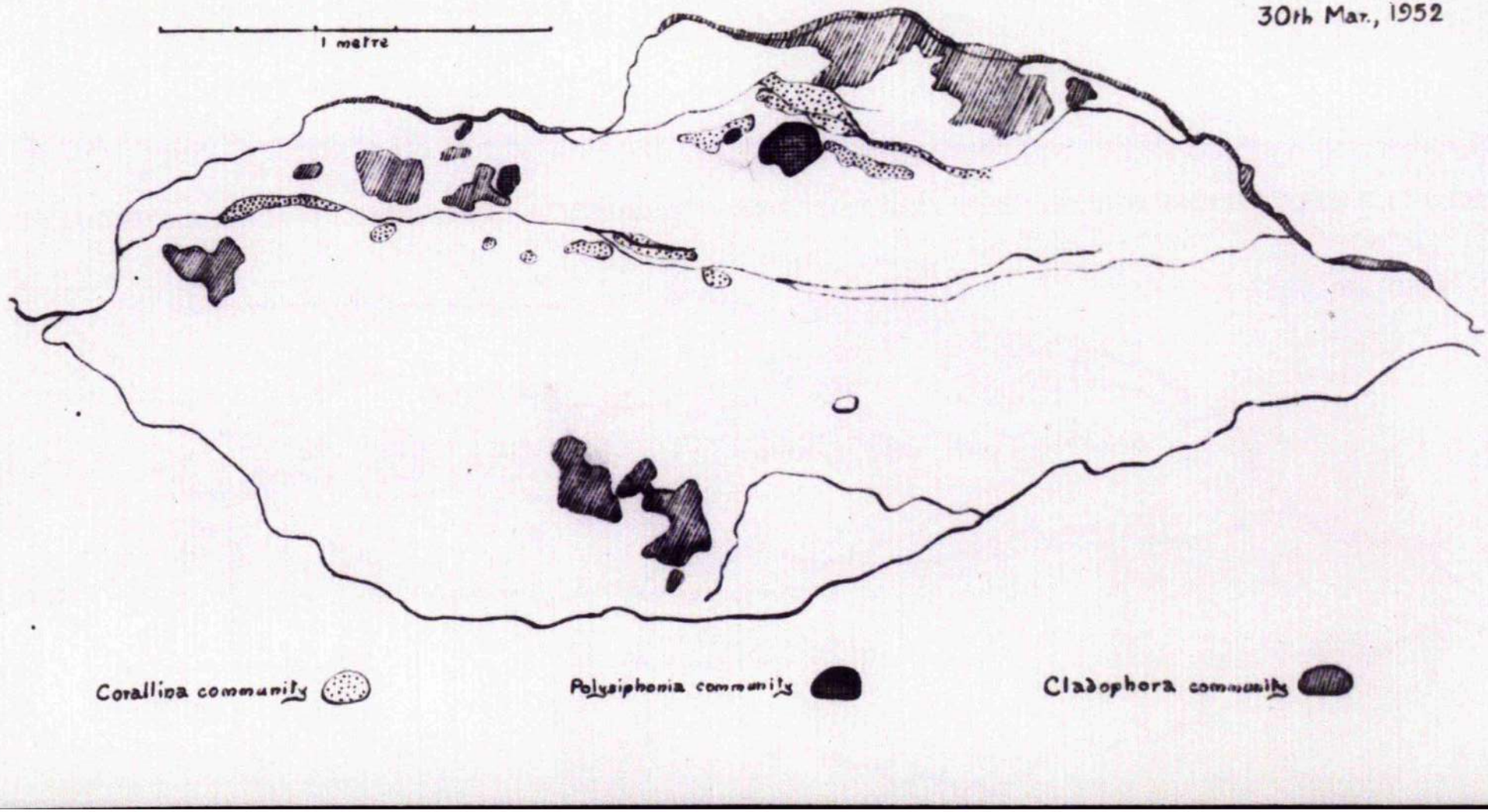

30th Mar., 1952
1 metre
Corallina community
Polysiphonia community
Cladophora community

PLATE IX. ALGAL COMMUNITIES

Fig. 15. Chart to show the configuration of the pool and size of the principal communities of perennial and pseudo-perennial plants within it in March 1954, for comparison with Fig.14. Large flakes of rock have broken away from the central ledge, the landward end, and from the floor of the pool on the northern side. The majority of the communities, particularly of Polysiphonia nigrescens, have not yet recovered from the destructive effects of conditions when the pool dried out completely during poor neap tides in March 1953.

26th Mar., 1954

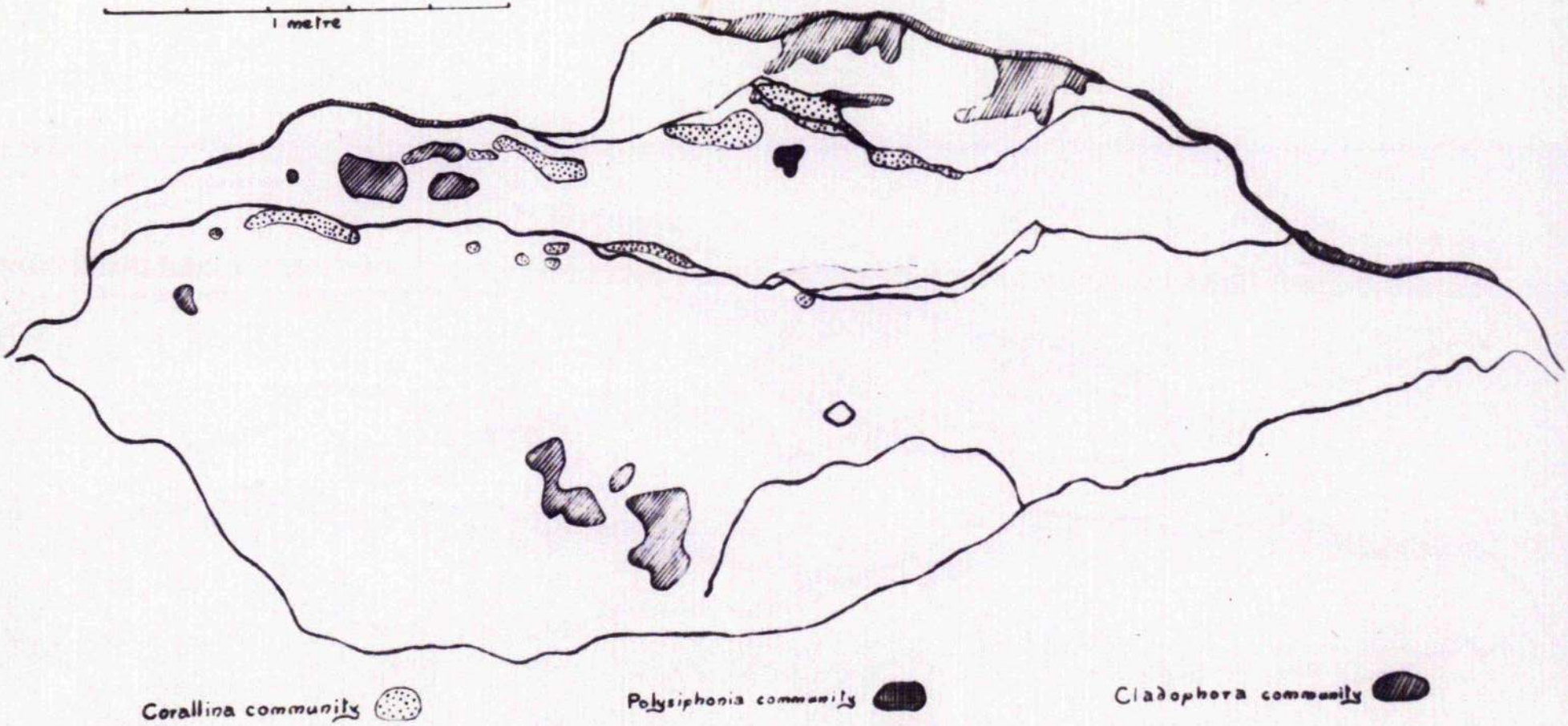
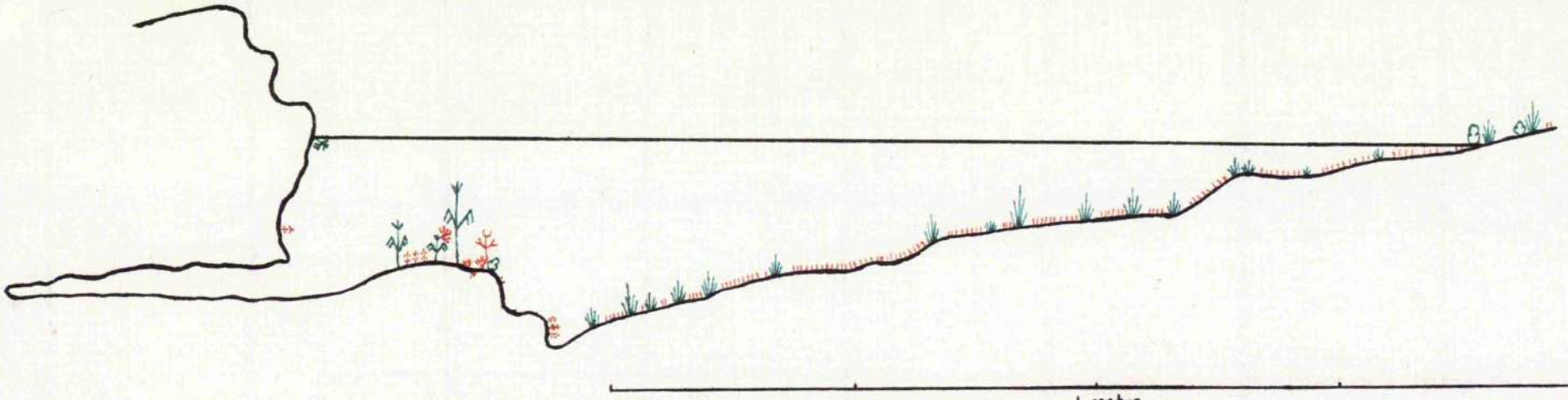


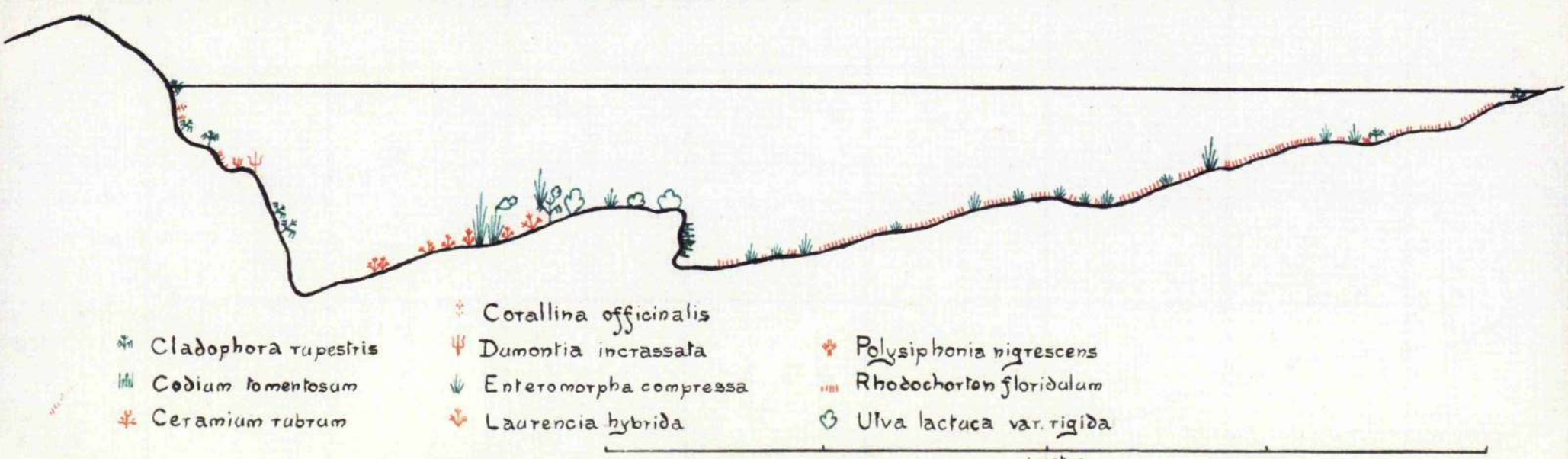
PLATE X. VEGETATION

Fig. 16. Transverse transect, seaward end, December 1950, with algae represented diagrammatically but to scale.

17. Transverse transect, centre of pool, December 1950, as Fig. 16.



1st. TRANSECT (DECEMBER)

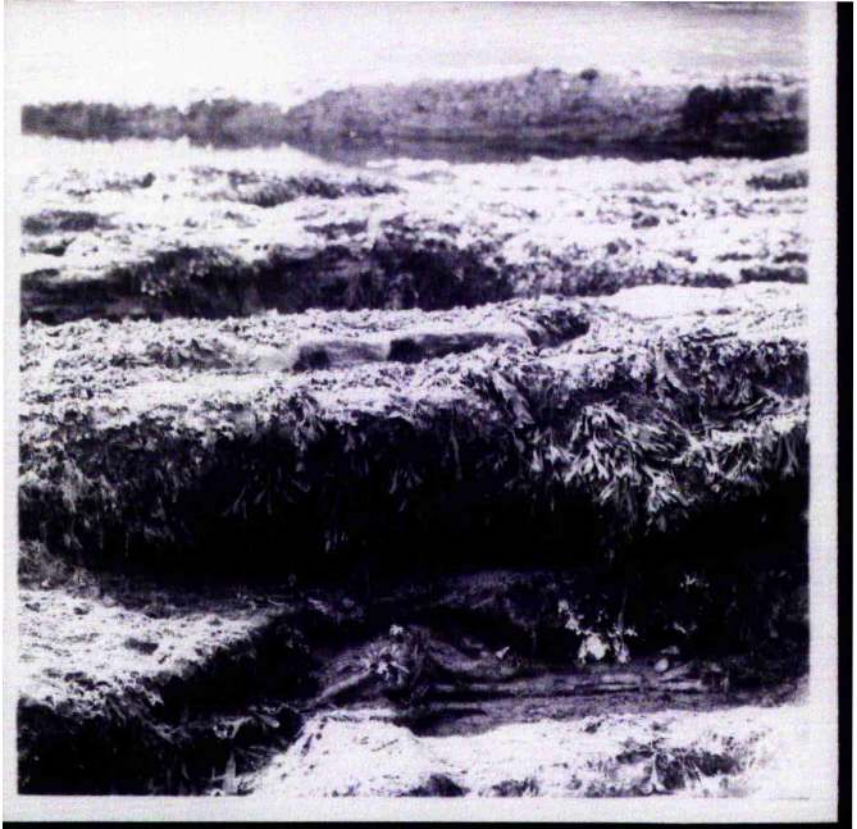


2nd. TRANSECT (DECEMBER).

PLATE XI. VEGETATION

Fig. 18. Part of the southern bank of the pool while dried out, 25th March 1953, showing the exposed micro-zone of Fucus spiralis and F. vesiculosus above the normal water line and the fringe vegetation of Cladophora rupestris at and below it (particularly to the left of the photograph).

19. Part of the northern bank of the pool with slightly lowered water level, 5th March 1953, showing the exposed micro-zone of small plants of Fucus spiralis above the normal water line, with a strong growth of Enteromorpha spp. at and below it (fringe micro-zone).



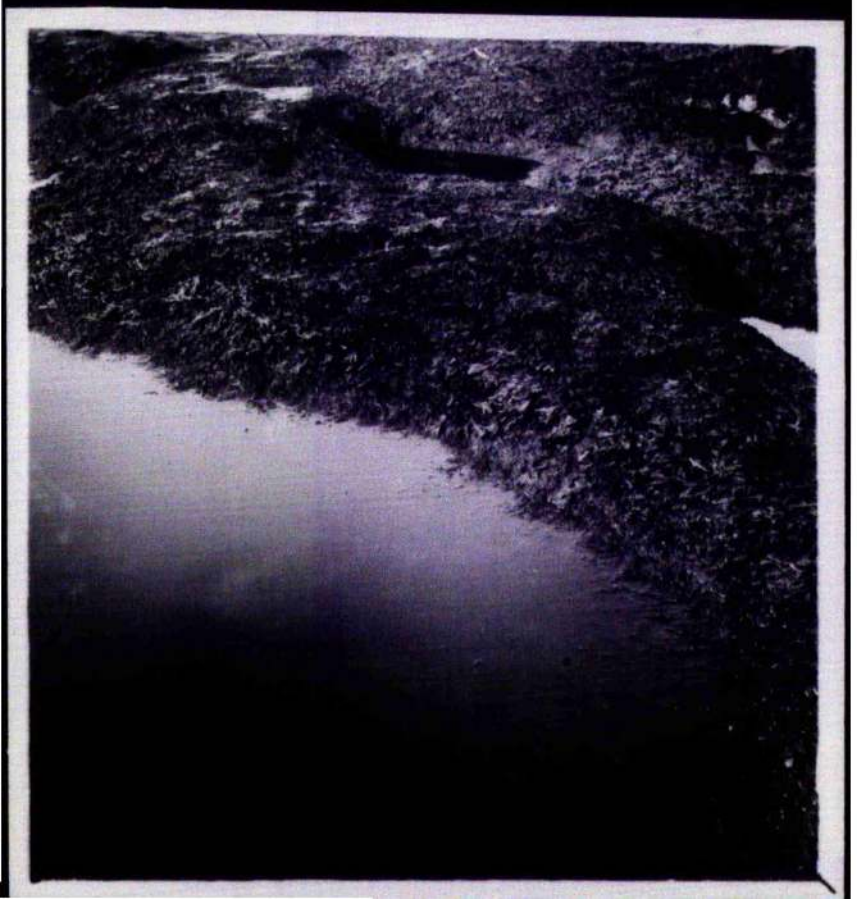


PLATE XII. VEGETATION

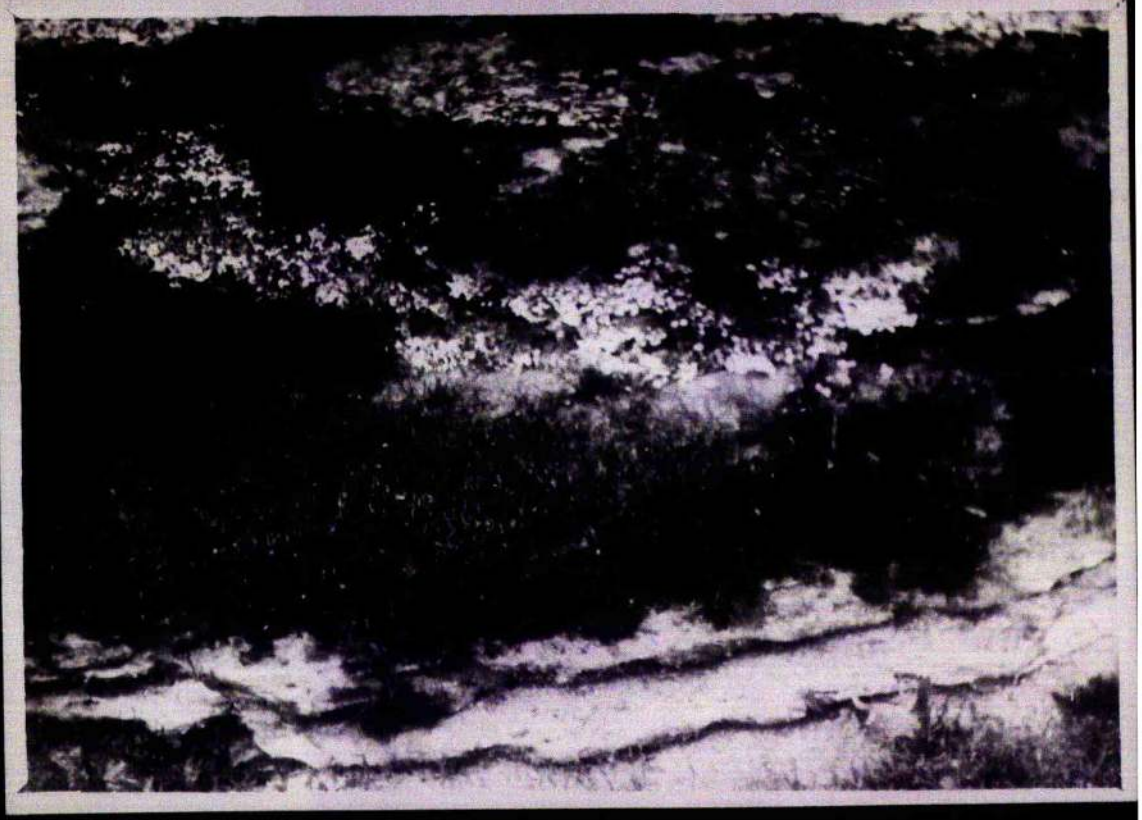
Fig. 20. Pool from landward end, 12.50 hrs., 22nd May 1953, showing the ephemeral Enteromorpha vegetation of the open-pool micro-association (mainly E. intestinalis and E. compressa) at its optimum state of development. A patch of plants of Ulva lactuca var. rigida killed by neap tide exposure can be seen in the foreground.

21. Pool from southern side, 8th February, 1953, the open pool being dominated at this season by Rhodochorton floridulum, while Enteromorpha specimens are small and sparsely scattered.

PLATE XIII. VEGETATION

Fig. 22. Vegetation of the deep corner on the southern side, April 1951. A strong growth of Enteromorpha compressa grows beside the still luxuriant plants of the Polysiphonia nigrescens community (dark vegetation towards left of photograph). Behind, and on the vertical face of the ledge, lie patches of Corallina officinalis, partly bleached by unfavourable neap tide conditions earlier in the month.

23. Vegetation of the deep corner on the southern side while the pool was dried out, 10.30 hrs., 25th March 1953. The flourishing community of Polysiphonia nigrescens (lower right) was completely destroyed by this exposure.



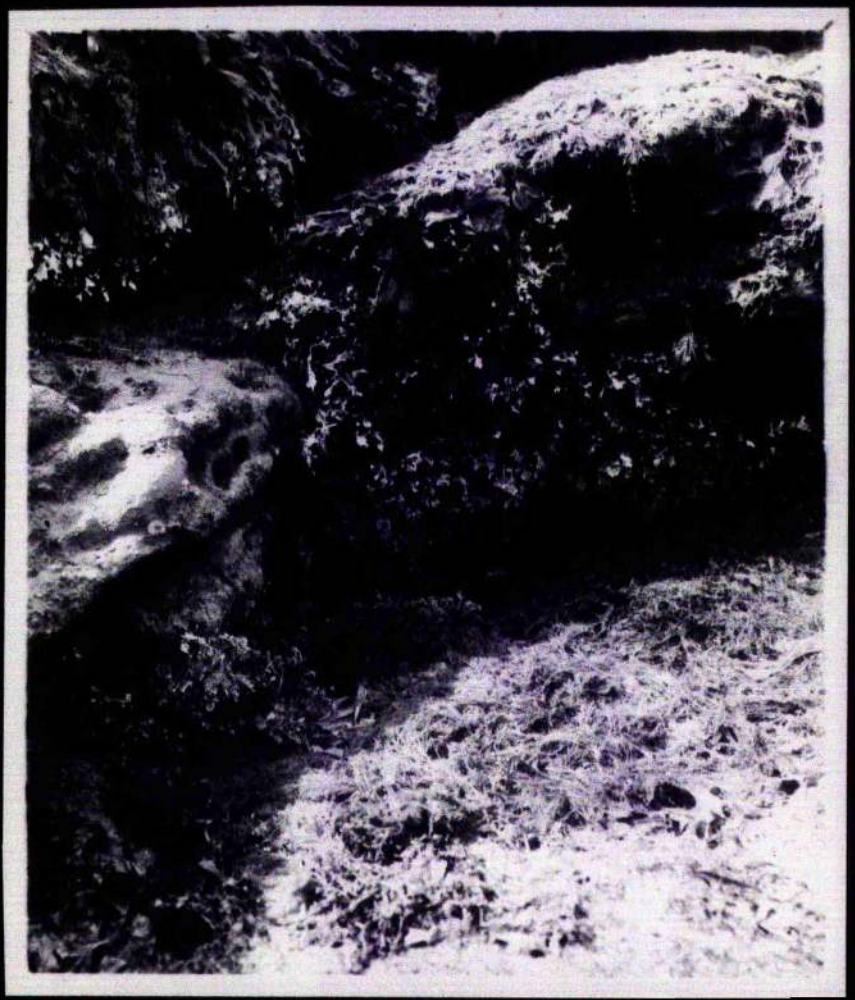


PLATE XIV. VEGETATION

Fig. 24. Southern part of the pool, March 1953, showing the dense growth of rather small Enteromorpha plants characteristic of early spring.

25. Enlargement of section of Fig.24 to show the vegetation of the central ledge, in this case Corallina officinalis with epiphytic Sphacelaria pennata var. fusca.

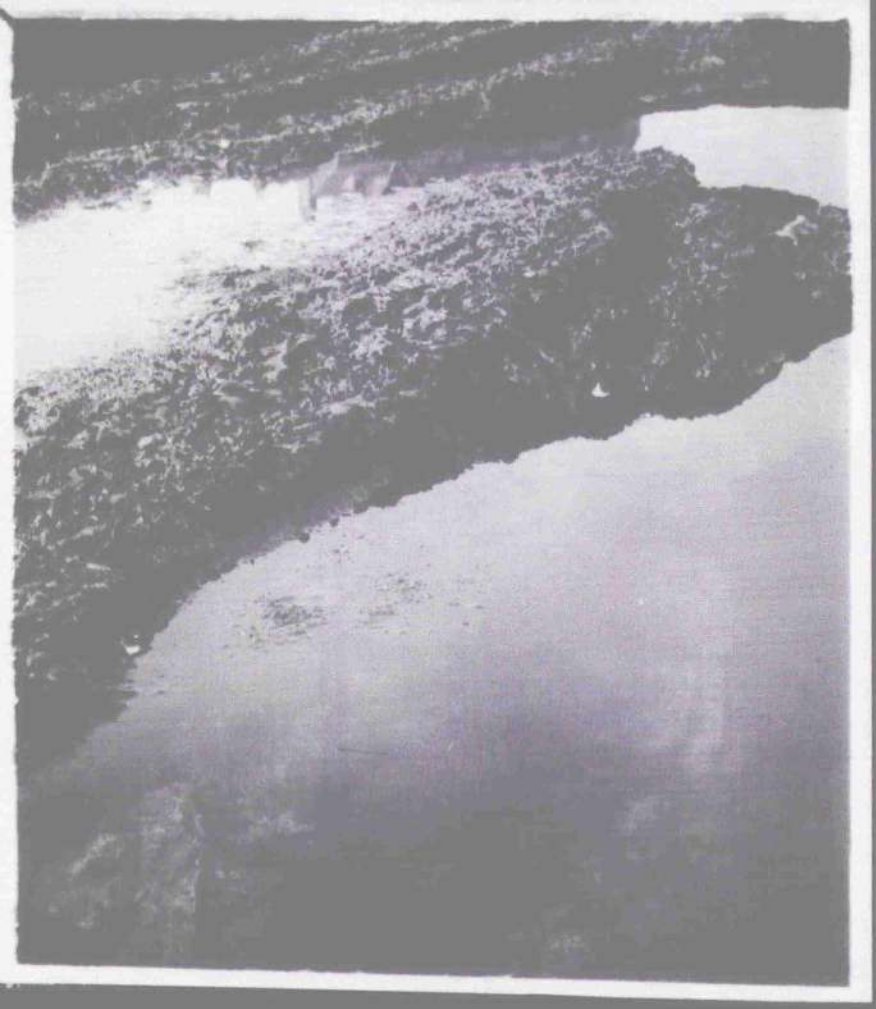


PLATE XV. DESTRUCTIVE EFFECTS OF POOR NEAP TIDES

Fig. 26. Landward end of pool, 8th April 1953, showing destruction of Ulva lactuca var. rigida caused by exposure while the pool was dried out. The dead plants are bleached, and are mixed with a relatively little affected growth of Enteromorpha spp., although the Enteromorpha plants of the fringe have been largely killed.

27. Seaward end of pool, 8th April 1953, showing white patches of algae killed by neap tide exposure two weeks previously.

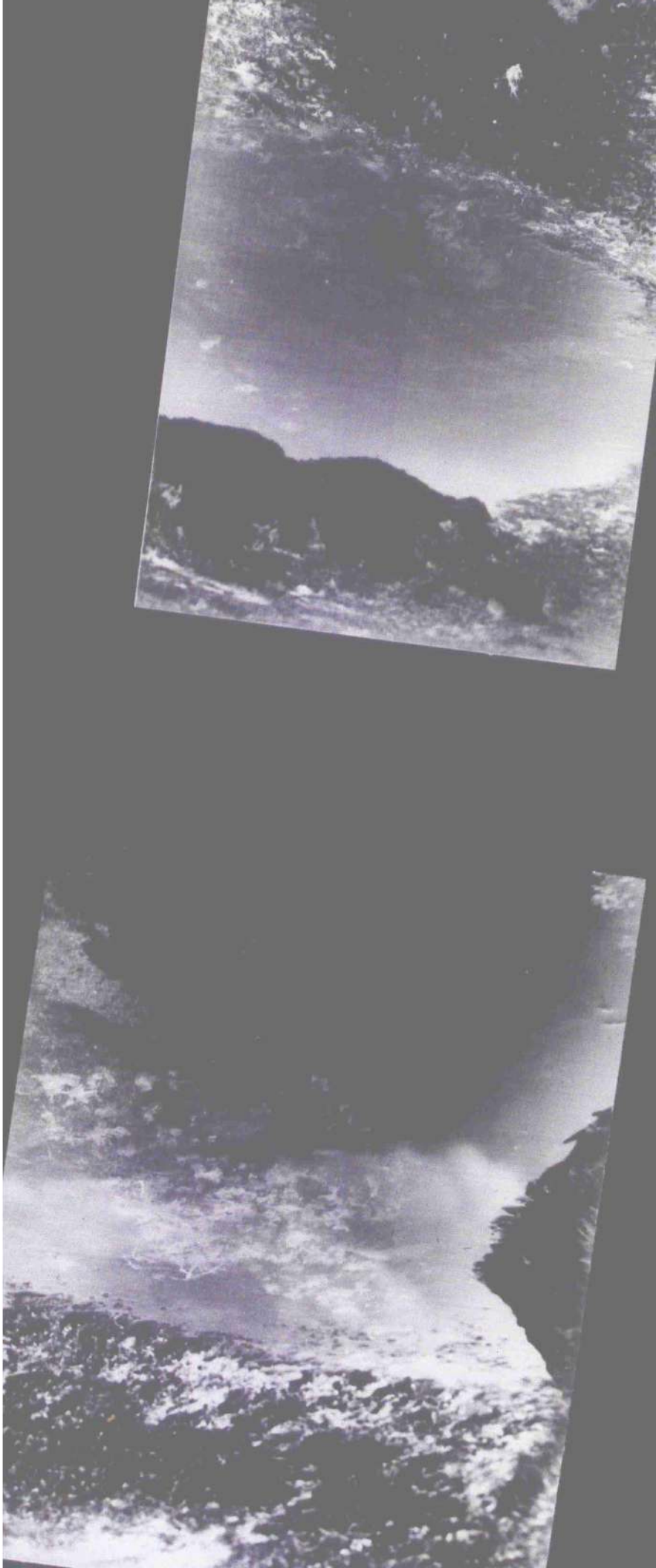
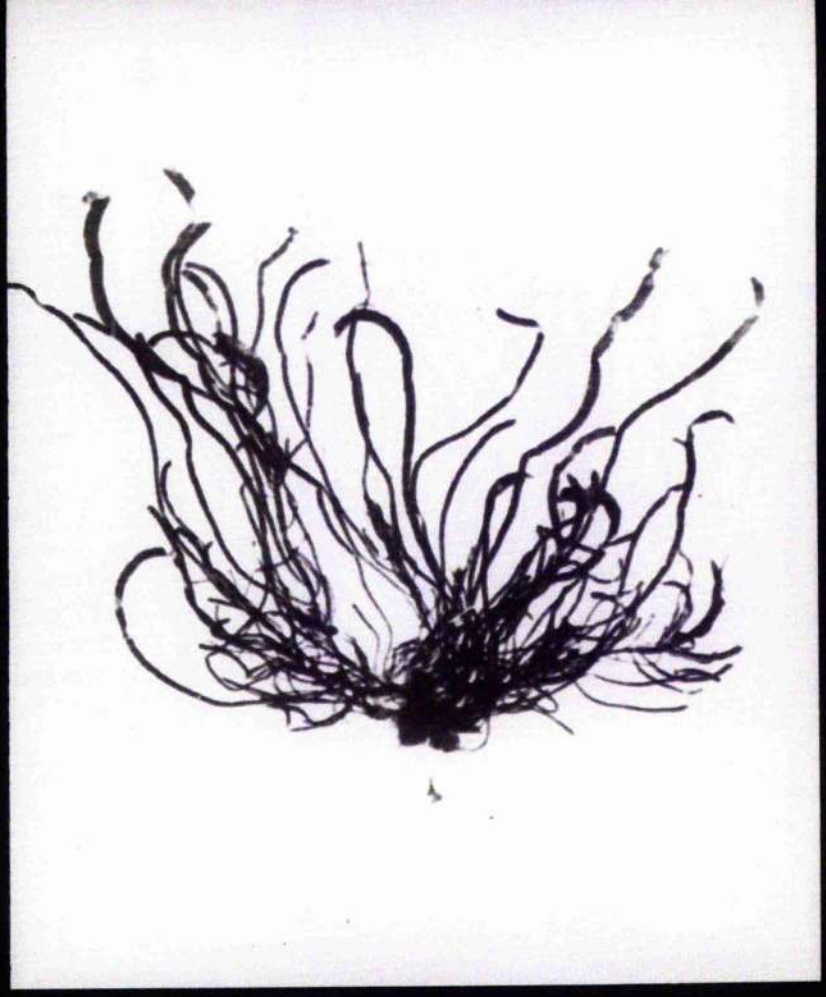


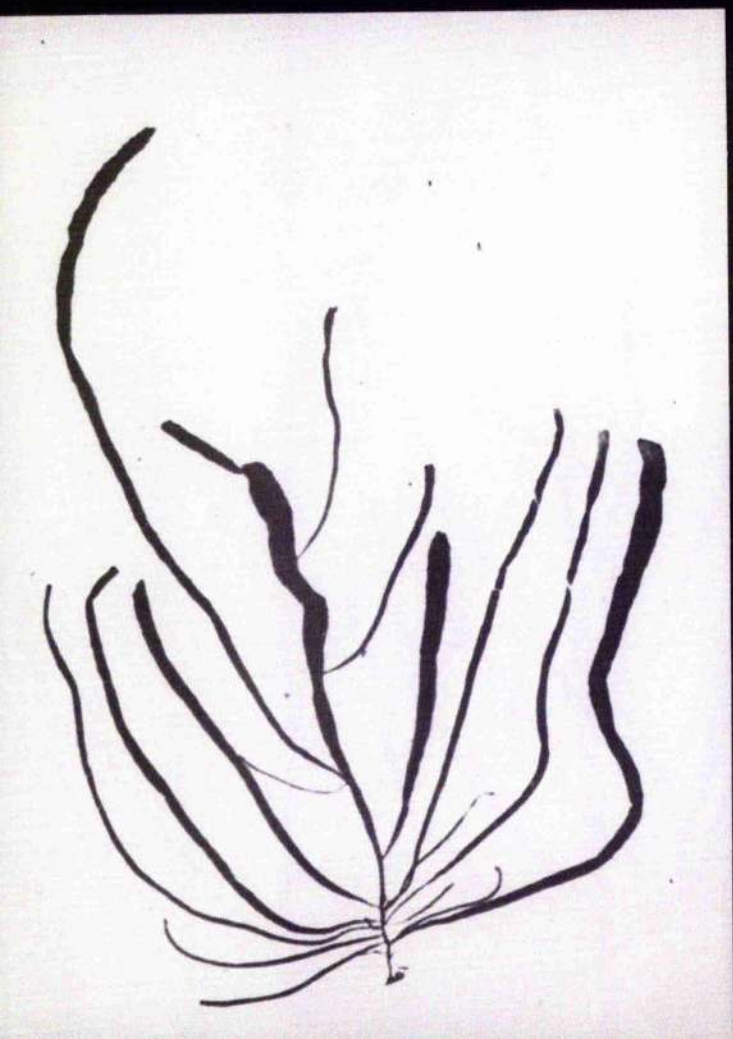
PLATE XVI. ENTEROMORPHA COMPRESSA (L.) GREV.

Fig. 28. Winter form November 1951, x 4/3.

29. Autumn form, on Cladophora rupestris, September 1953, x 5/4.

30. Early summer form, May 1952, x $\frac{1}{3}$.





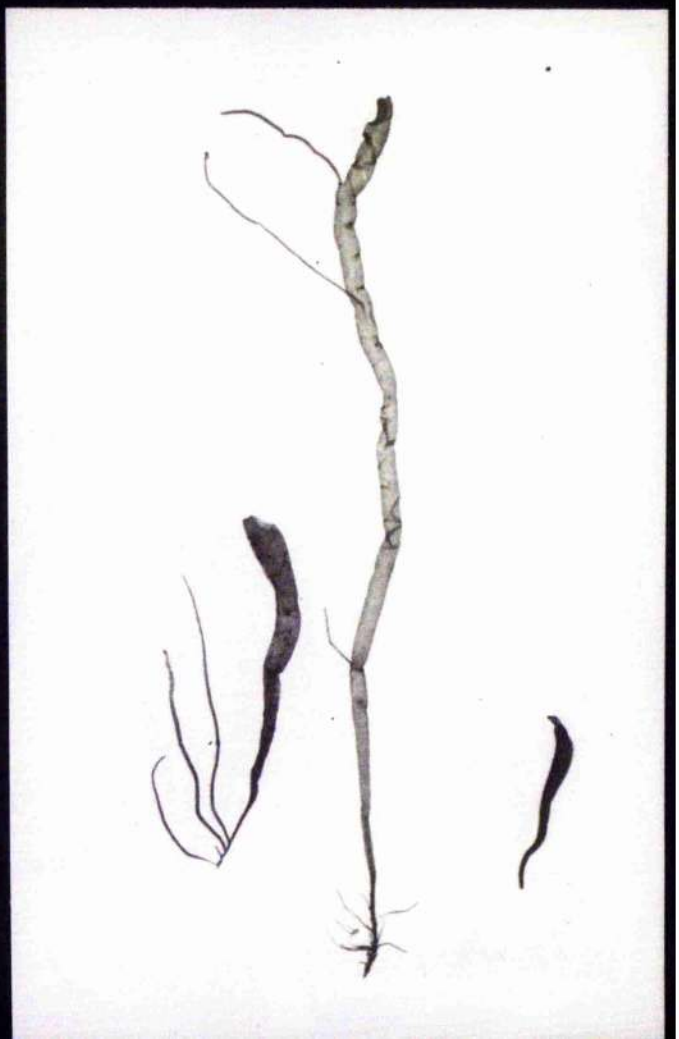
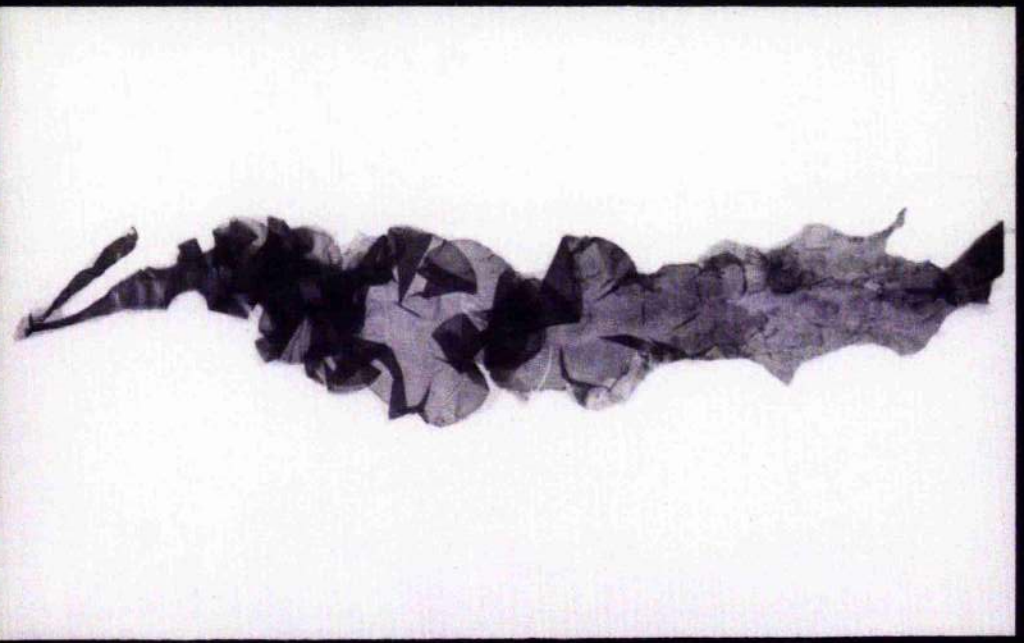


PLATE XVII. ENTEROMORPHA SPP.

Fig. 31. Enteromorpha intestinalis (L.) Link.
March 1952, x ½.

32. E. linza (L.) J. Ag. May 1952, x 2/5.



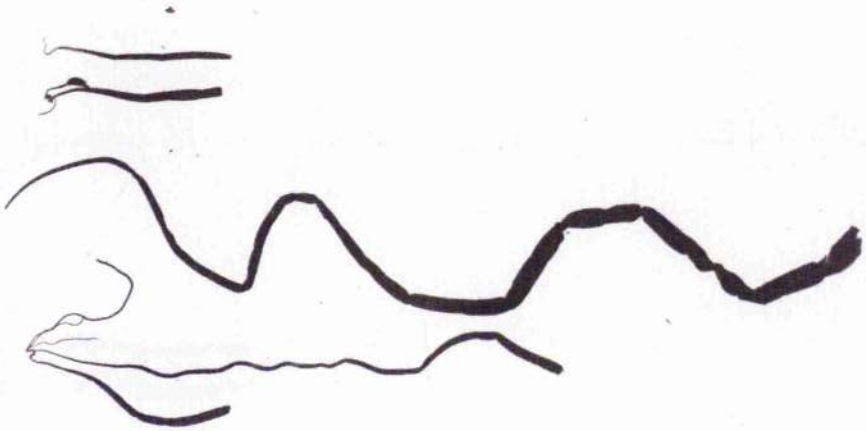
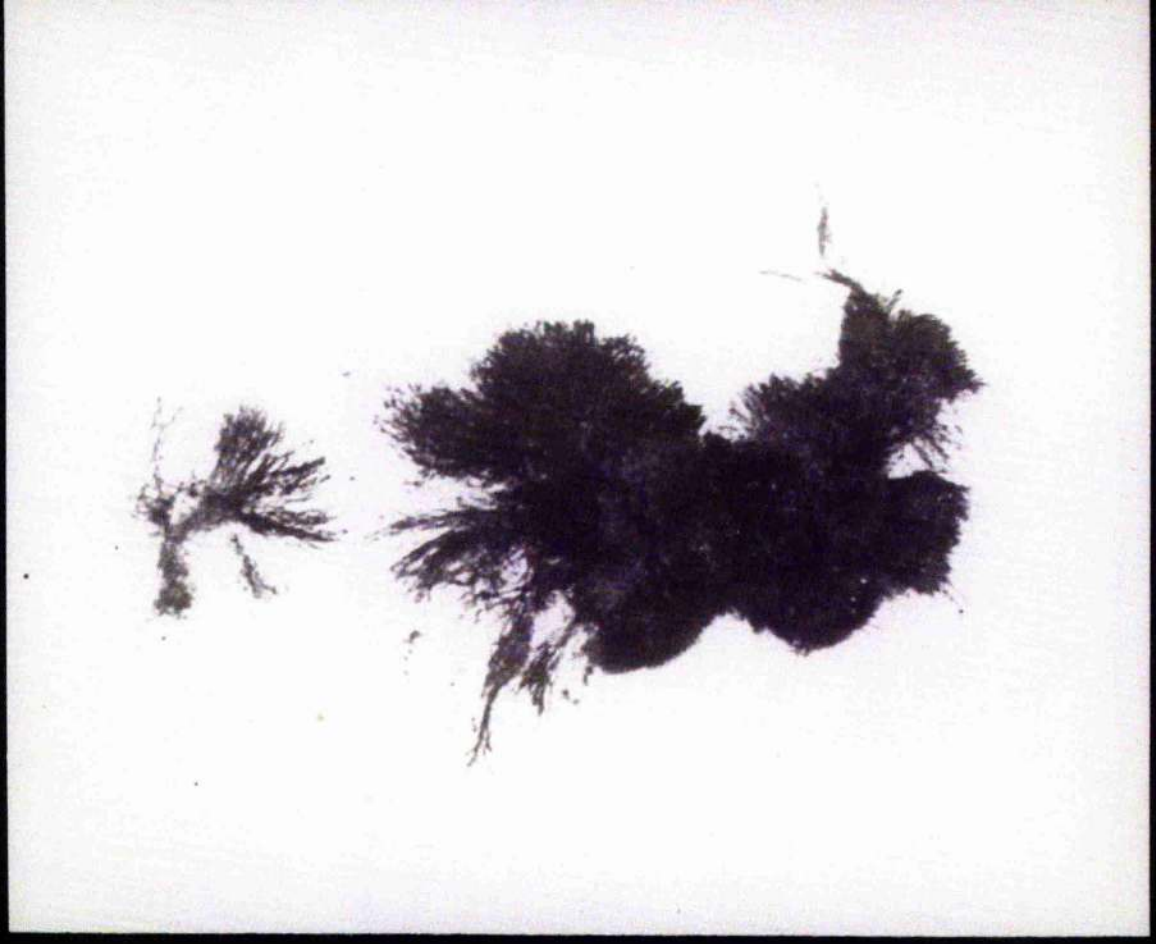


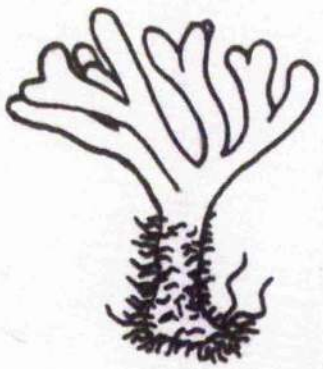
PLATE XVIII. *CODIUM TOMENTOSUM* STACKH.

Fig. 33. Typical non-thalloid growth from central ledge of pool, October 1953, x 4/5.

34. Well-developed thallus from a neighbouring pool, natural size.

35. Two fully-formed utricles and a filament beginning to form a branch, x 90.





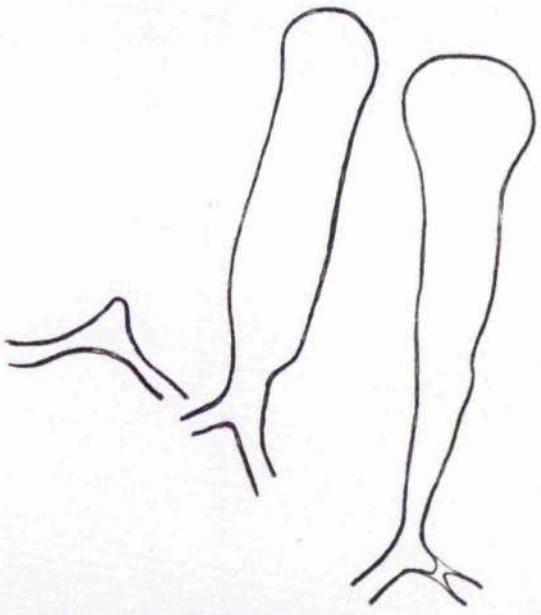
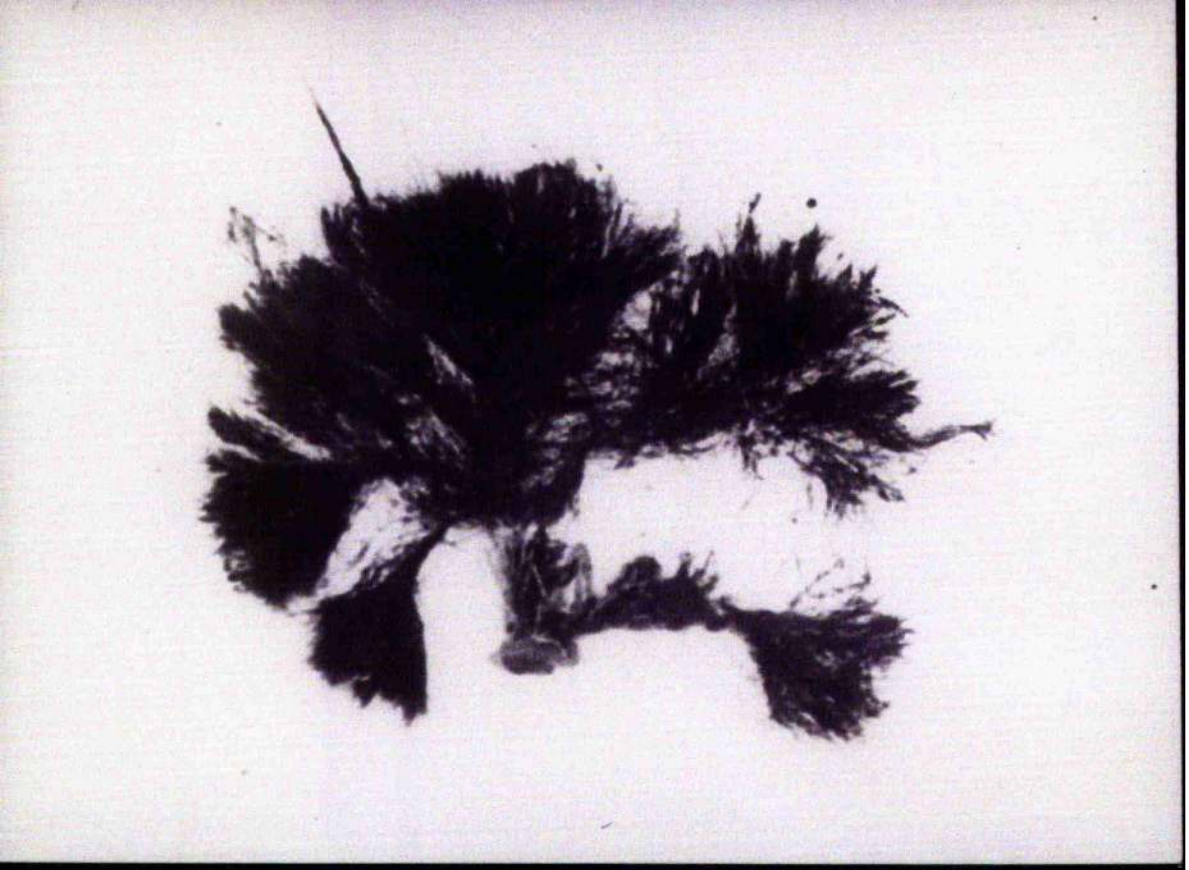


PLATE XIX. SPHACELARIA PENNATA (HUDS.) LYNGB. VAR. FUSCA COMB. NOV.

Fig. 36. Well-developed growth on Corallina officinalis, September, 1952, natural size.

37. Propagules at various stages of development, August 1950, from a preparation, x 34.



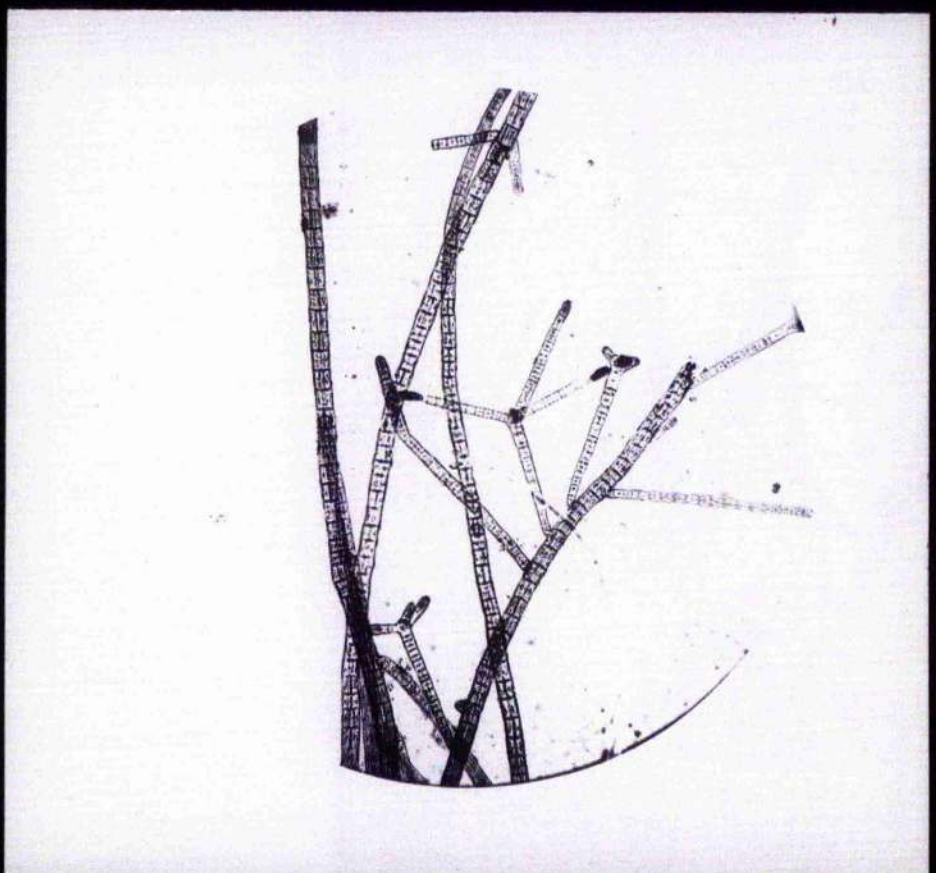
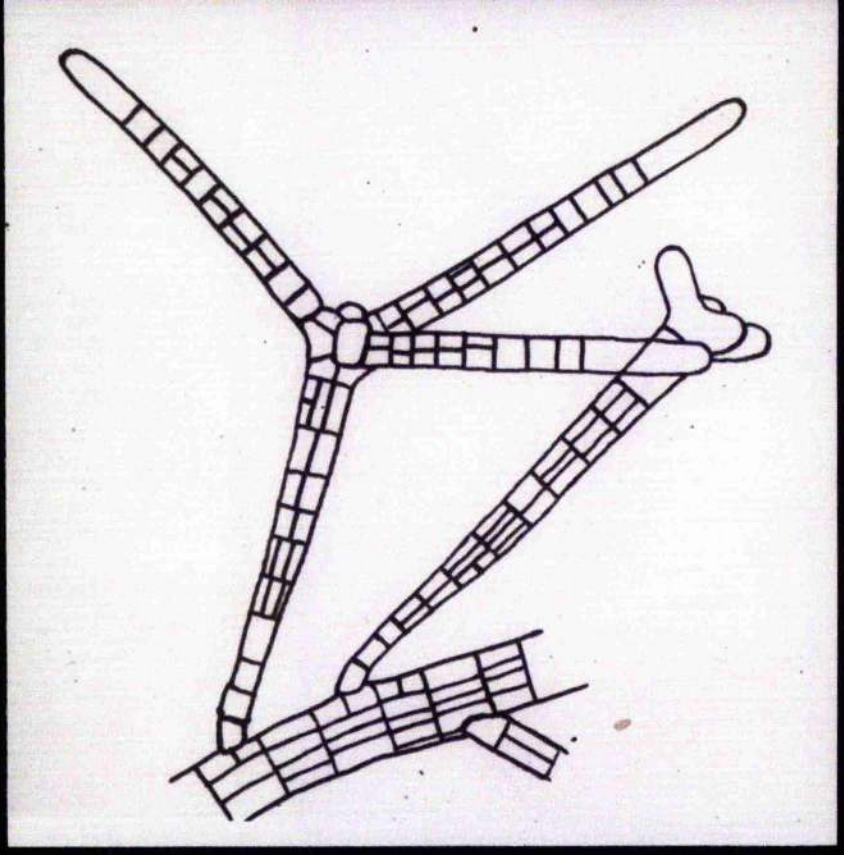


PLATE XX. SPHACELARIA PENNATA VAR. FUSCA

Fig. 38. Drawing of propagule from preparation of fig. 37 to show detailed structure more clearly, x 135.

39. Drawing of unilocular sporangia on plant of December 1953, showing innovation of new sporangia from the bases of those which have dehisced, x 140.



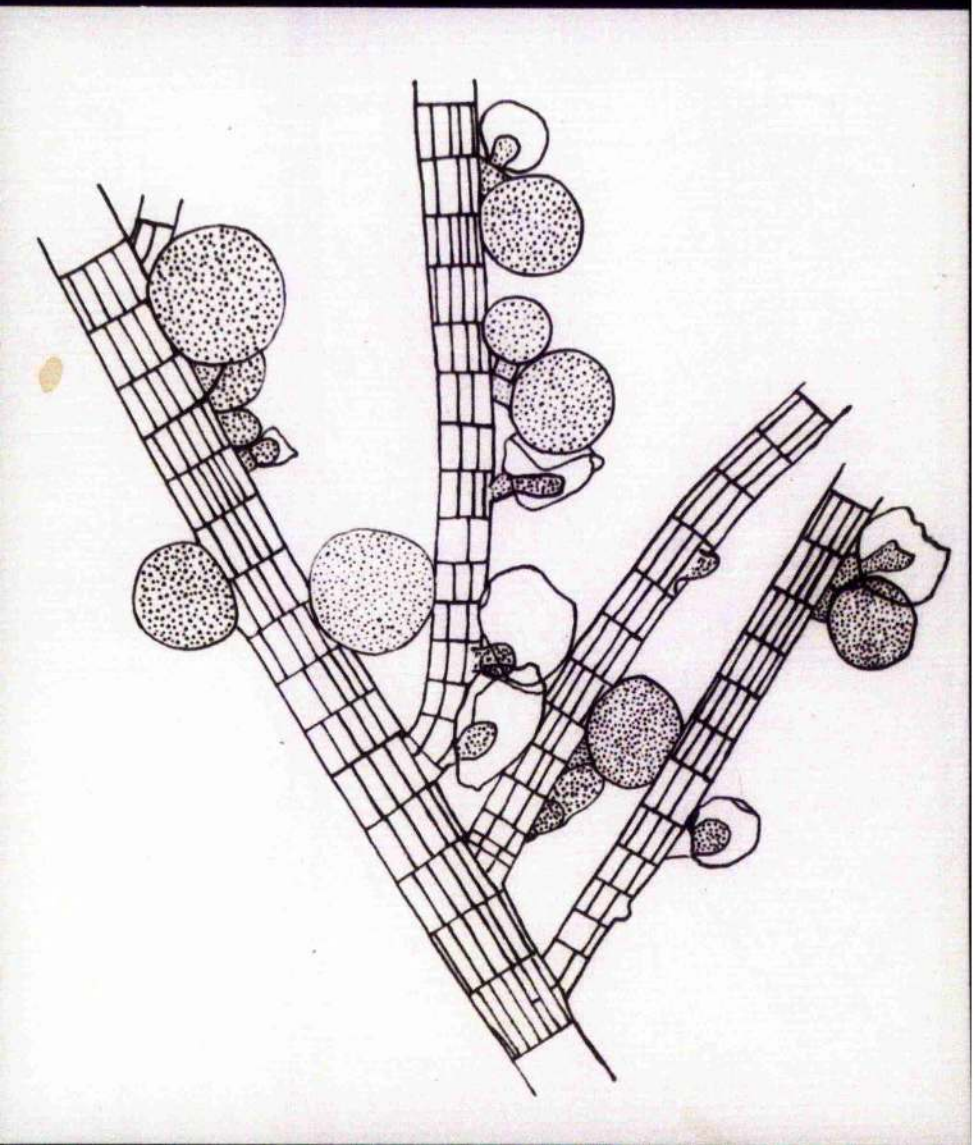
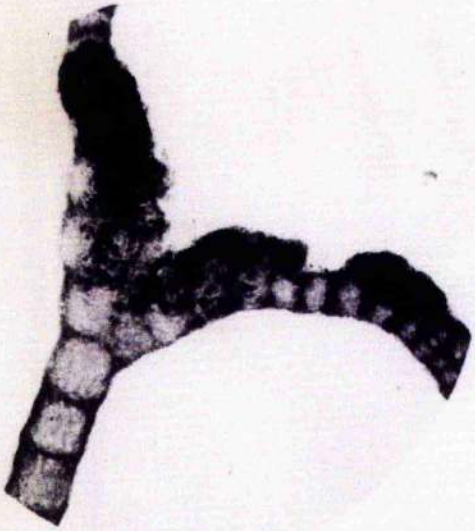


PLATE XXI. GALLS ON *CERAMIUM RUBRUM*

Fig. 40. Old and extensive galls containing masses of tetraspores continuous with those at the nodes of the normal tissues, December 1953, x 30.

41. Early stage of gall, with regular, more or less spherical form, not containing any tetraspores, although the plant is tetrasporiferous, October 1951, x 150.



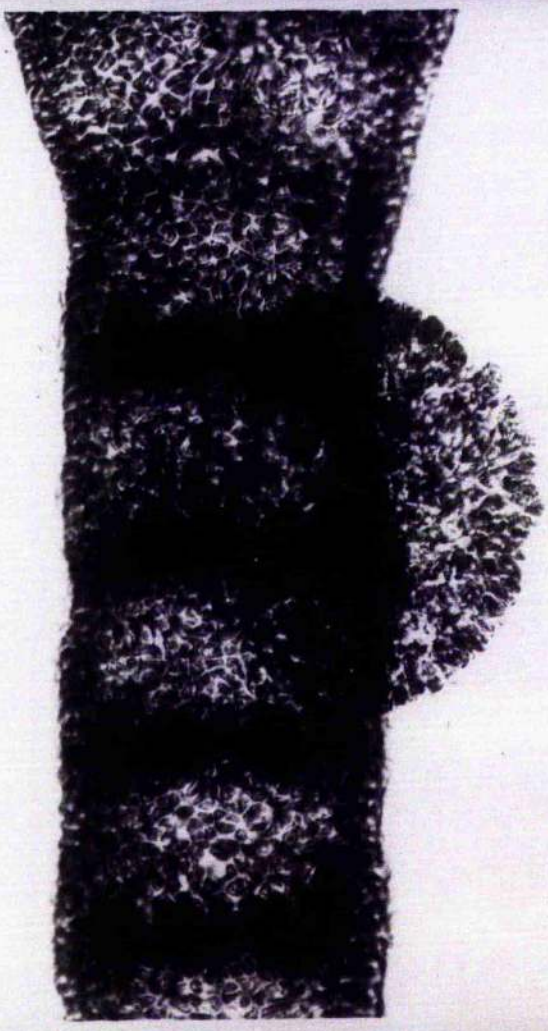
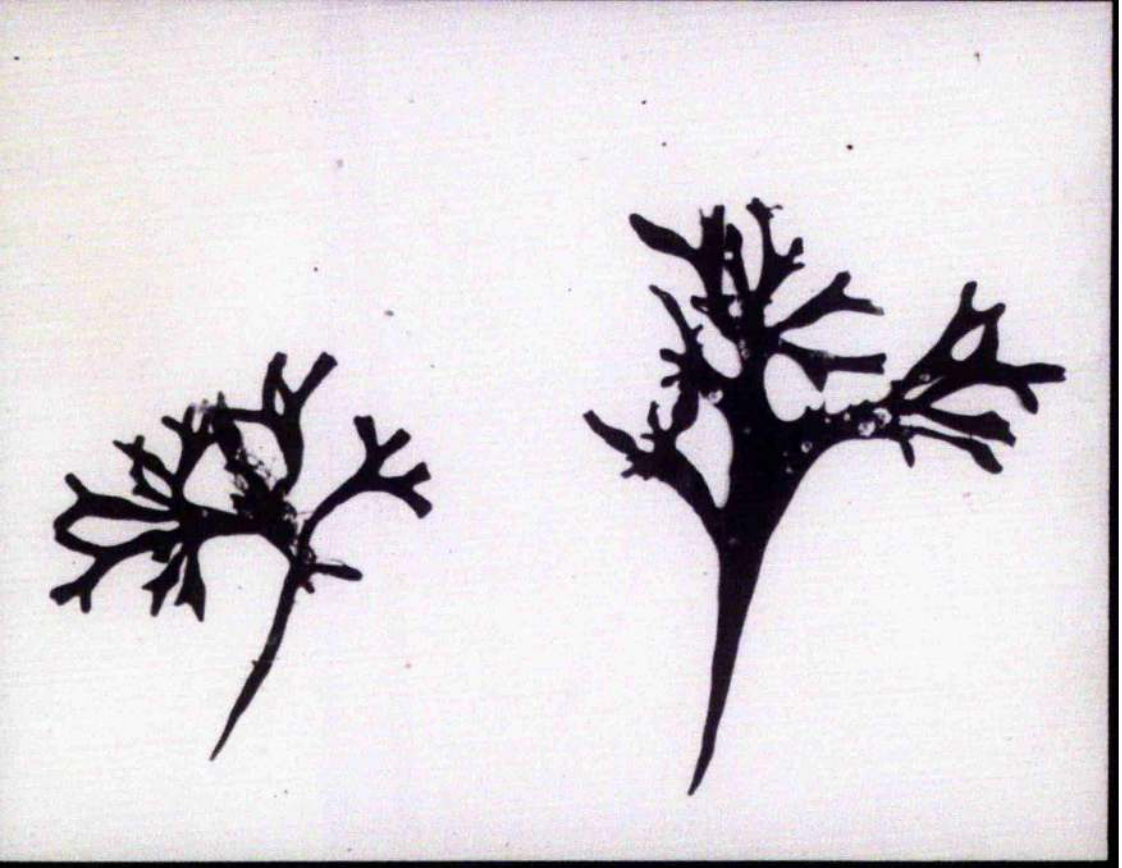


PLATE XXII. EPIPHYTISM

Fig. 42. Chondrus crispus (L.) Stackh. Plants growing in the open pool amongst Cladophora rupestris (left) and in the deeper, shady part of the pool (right), October 1951, natural size, to show the relatively reduced form and proneness to settlement by epiphytes of the former.

43. Enteromorpha sporelings which have developed in abundance on dead tissues of Cladophora rupestris, May 1953, x 18. Living parts of the plant are not affected nearly as heavily.



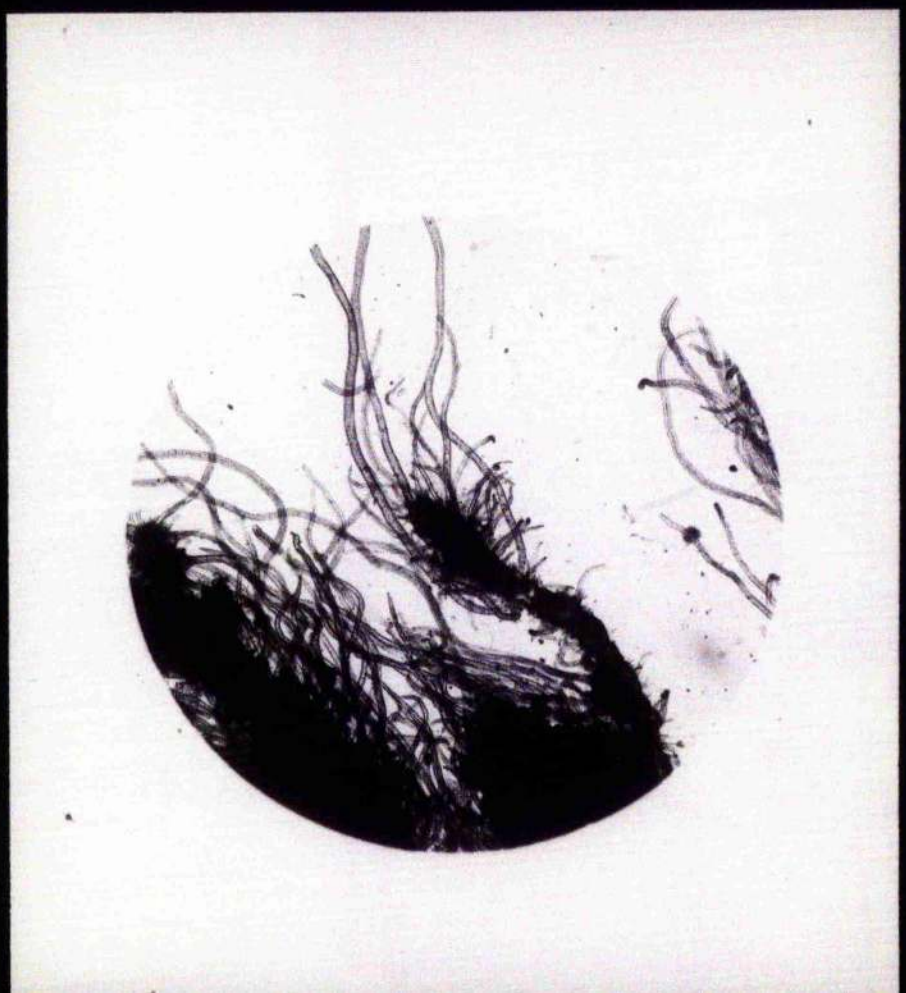
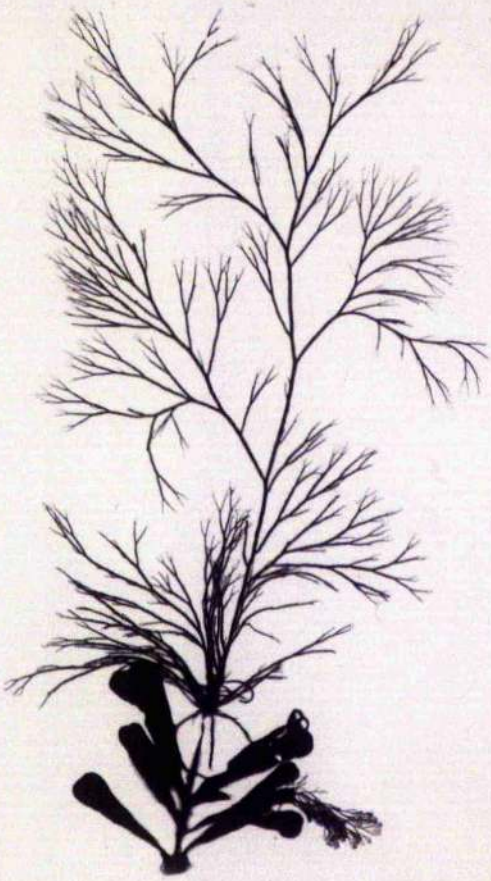


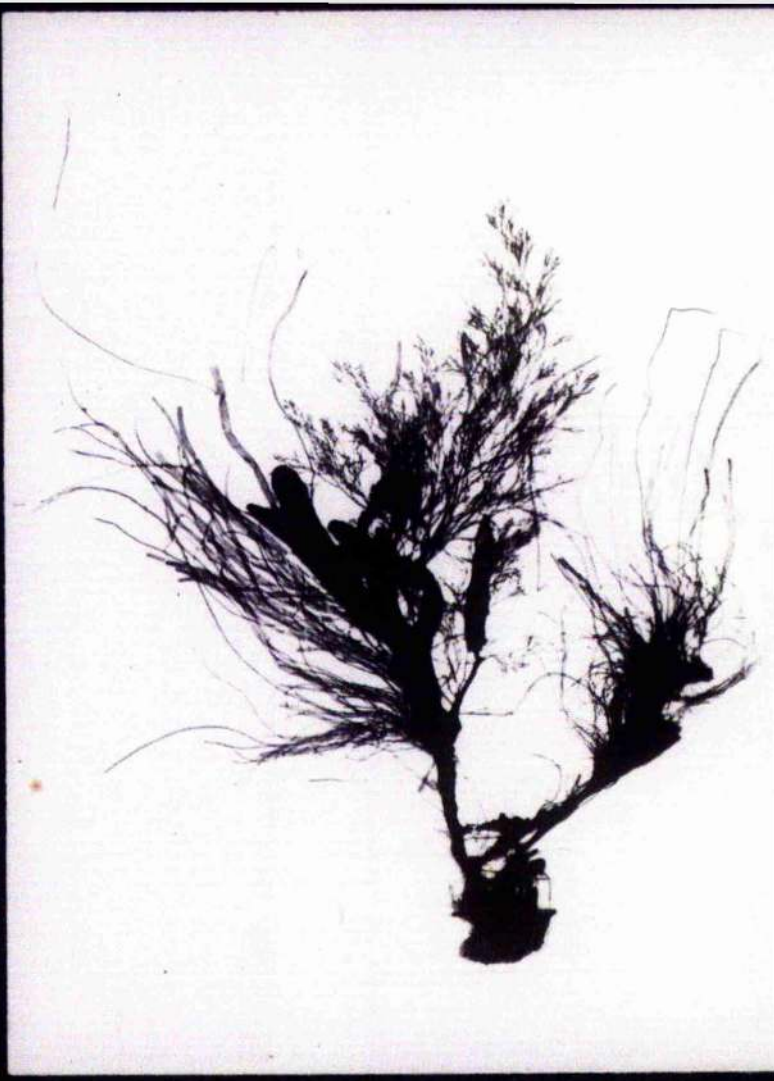
PLATE XXIII. EPIPHYTISM

Fig. 44. Large tetrasporiferous plant of Ceramium rubrum epiphytic on a small Fucus plant, February 1952, x 3/5. The greatly increased strain on the holdfast of the latter is obvious.

45. A heavy growth of Ceramium rubrum and Enteromorpha compressa on a Fucus plant, September 1951, x $\frac{1}{3}$.

46. Polysiphonia nigrescens (Sm.) Grev., September 1952, x 3/4.
The old, perennial fronds are covered with epiphytic Ceramium rubrum, Enteromorpha compressa and diatoms, and the regeneration of late autumn and winter has not yet begun.





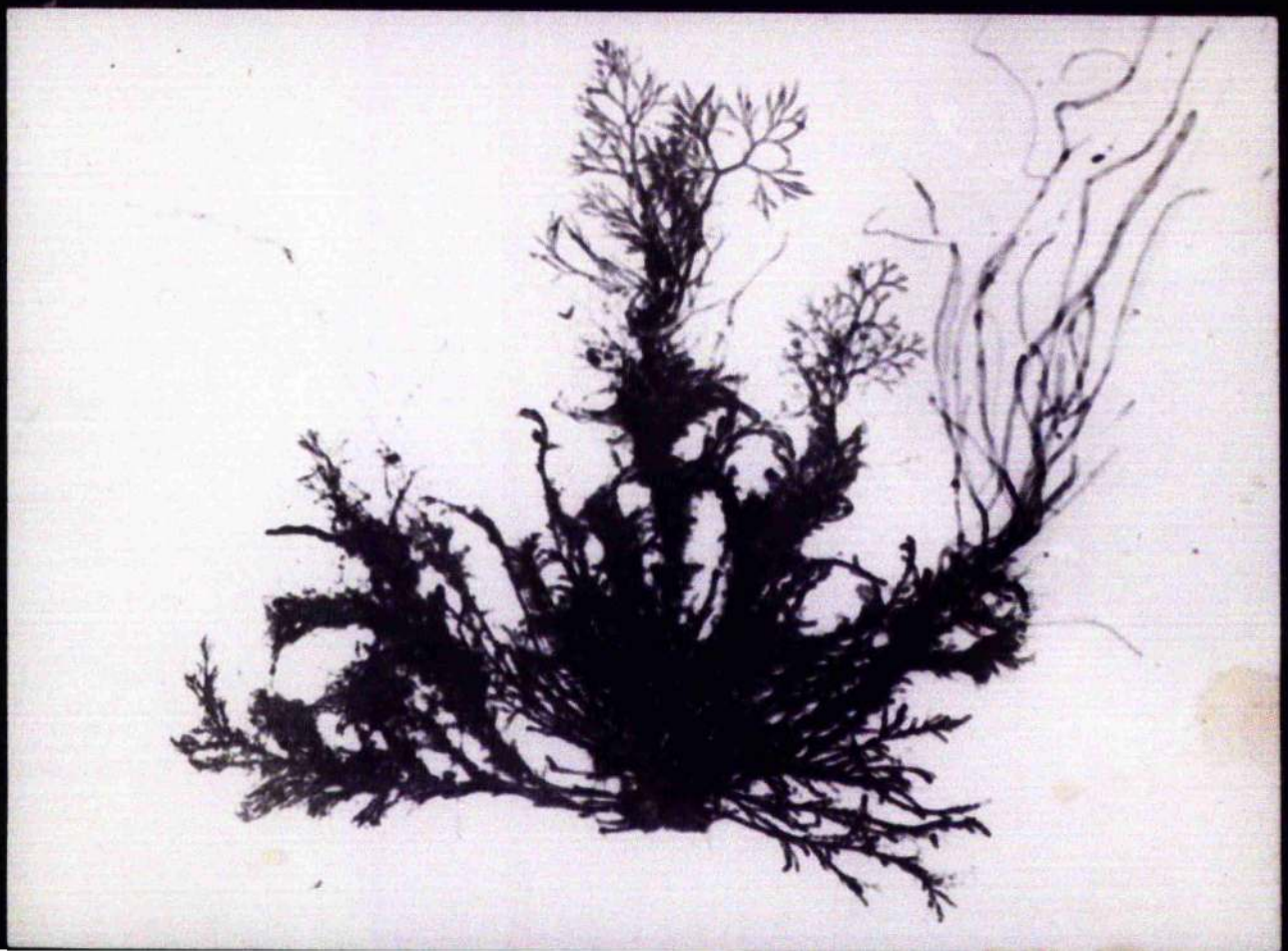


PLATE XXIV. EPIPHYTIC DIATOMS

Fig. 47. The tip of a young plant of Dumontia incrassata overgrown with Licmophora paradoxa and very young Ceramium rubrum, November 1950, x 18.

48. A similar growth of Licmophora sp. and entangled filaments of Rhizoclonium implexum on Sphacelaria pennata var. fusca, itself growing on Cladophora rupestris, September 1953, x 19.

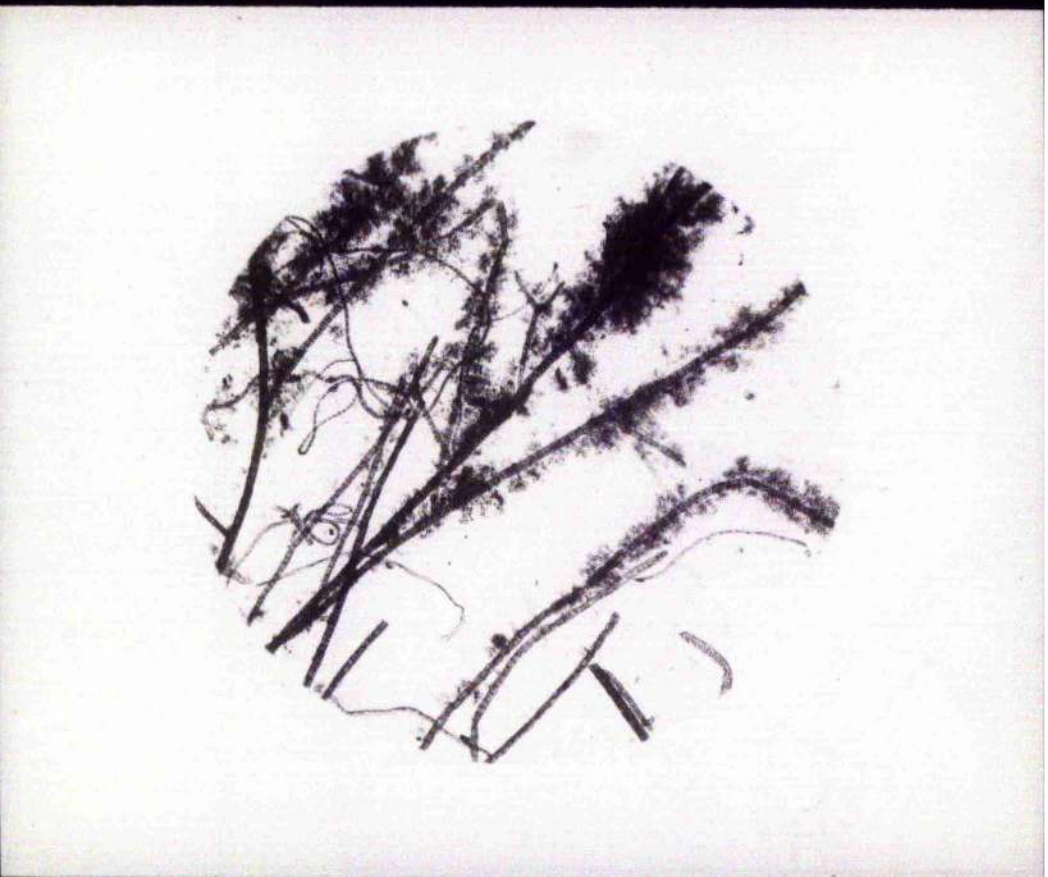


PLATE XXV. INTER-RELATIONSHIPS OF PLANTS AND ANIMALS

Fig. 49. Nematode with ingested diatoms, from silt amongst Rhodochorton floridulum, November 1950. The larger diatom is 50 μ long.

50. Fabricia sabella Ehrenberb, x 25. The fixation of silt by the mucus of this little polychaete appears to be an important factor in determining the nature of the substratum of the pool.